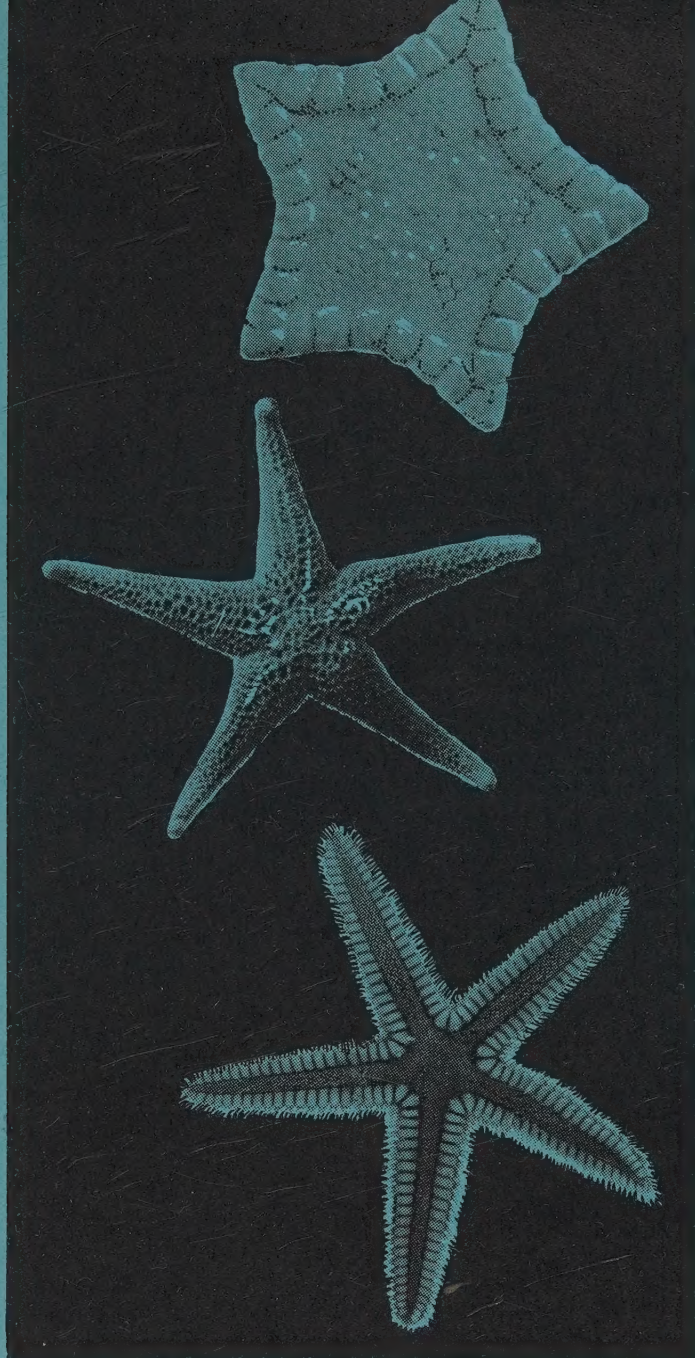


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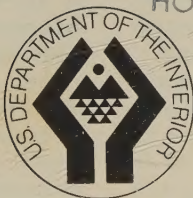
UNITED STATES DEPARTMENT OF THE INTERIOR

U.S. FISH AND WILDLIFE SERVICE

BUREAU OF COMMERCIAL FISHERIES

FISHERY BULLETIN

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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.

SEASONAL DEPTH DISTRIBUTION OF FISH IN SOUTHEASTERN LAKE MICHIGAN

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ABSTRACT

This study is based on systematic seasonal bottom trawling between 3 and 50 fathoms (5.5 and 91.5 m.) from February to November 1964 and supplementary information from other experimental fishing at additional depths and with other gear. The seasonal depth distribution of eight common species is described, and temperature relations are discussed. Catch records for less common species are mentioned briefly.

Alewives are mostly pelagic during their first 2 years, but many young of the year are on the bottom in the fall, and yearlings occasionally descend to the bottom in substantial numbers in the spring and fall. Adults are mostly on the bottom in the winter and spring, but a significant portion of the population may be at mid-levels in the summer and fall. Bloaters are in midwater during their first 2 years, but usually on the bottom thereafter. Young-of-the-year American smelt are in midwater except in the fall, yearlings are in midwater or on the bottom, and adults are mostly on the bottom.

Alewives, bloaters, smelt, spottail shiners, trout-perch, and yellow perch on the bottom moved into shallower water in the spring and into deeper water in the fall, in response to temperature changes. Slimy sculpins abandoned inshore areas as water warmed in the spring. Fourhorn sculpins showed a slight movement shoreward in the spring, but changed their depth

distribution little thereafter to the end of the trawling season.

Alewives showed the greatest seasonal change in distribution. Large concentrations at 40 to perhaps 70 fathoms (73.2–128.0 m.) in mid-March had migrated to water of less than 15 fathoms (27.4 m.) by mid-April. They were in shallow water along shore or in rivers until early summer; then they began a postspawning movement back into deeper water which continued into the fall. Depth ranges in which greatest numbers of other common species occurred, considering all seasons as a whole, were as follows: bloater, 12 to 50 fathoms (21.9–91.5 m.); American smelt, 5 to 17 fathoms (9.1–31.1 m.); spottail shiners, 3 to 15 fathoms (5.5–27.4 m.); trout-perch, 5 to 17 fathoms (9.1–31.1 m.); yellow perch, 3 to 15 fathoms (5.5–27.4 m.); slimy sculpins, 15 to 40 fathoms (27.4–73.2 m.); fourhorn sculpins, 45 to 70 fathoms (82.2–128.0 m.).

Water temperature ranges (° C.) in which the various species were most abundant in summer were: alewife, 8 to 22; bloater, 6 to 10; smelt, 6 to 14; spottail shiner, 13 to at least 22; trout-perch, 10 to 16; yellow perch, 11 to at least 22; slimy sculpin, 4 to 6; fourhorn sculpin, 4 to 4.5. Fluctuations in inshore water temperatures in the summer caused short-term changes in depth distribution.

Published records of depth distribution of fish in the Great Lakes have been limited largely to general information included as part of other studies. Data on seasonal aspects of distribution are especially scarce, although Dryer (1966) gave considerable information on seasonal changes in bathymetric distribution of fish in the Apostle Islands region of Lake Superior. His review of current literature on the depth distribution of Great Lakes fish need not be repeated here. The present paper describes the seasonal depth distribution of eight

of the most abundant species in Lake Michigan and gives information on the effect of temperature on depth distribution, especially during the summer.

METHODS AND MATERIALS

Data were obtained from bottom tows with a semiballoon trawl in 1964 off Saugatuck, Mich. This net had a 39-foot (11.9 m.) headrope, 51-foot (15.5 m.) footrope, and a cod end of ½-inch (1.3

cm.) mesh, extension measure. Series of tows (one haul at each of 14 depths) were made from the R/V *Kaho* in mid-February and mid-March, and from the R/V *Cisco* at about 3-week intervals from April 11 to August 21, in mid-October, and in early November. A "standard" series of tows consisted of bottom tows along the contour at 3, 5, 7, 10, 12, 15, and 17 fathoms (5.5, 9.1, 12.8, 18.3, 21.9, 27.4, and 31.1 m.) and at 5-fathom (9.1 m.) intervals from 20 to 50 fathoms (36.6 to 91.5 m.). Distances from shore of the sampling depths ranged from 0.4 to 16.7 nautical miles (0.7–31.0 km.) (table 1). Ice prevented the collection of samples at 3 fathoms (5.5 m.) in February and March. All tows lasted 10 minutes except those at 3 fathoms (5.5 m.) which lasted only 5 minutes, due to limited areas of suitable trawling bottom. The catches at 3 fathoms (5.5 m.) were adjusted to 10 minutes in all tabulations. All 14 tows of each standard series were made on the same day, with two exceptions (February 13 and 14; July 7 and 9), when tows at 45 and 50 fathoms (82.3 and 91.5 m.) were made 1 or 2 days after shallower tows. The dates "February 13" and "July 7" are used here in all further references to these series.

Engine speed was the same for all tows, and the trawling speed was about 2.6 knots. Variation in speed of tows during periods of significant wind was minimized by making all tows (which, to follow the bottom contours, were always either north

or south) with the wind on a stern quadrant. Currents along the shore in the study area are highly responsive to wind and ordinarily flow north or south according to the wind. We did not trawl during periods of high winds.

Bathythermograph casts were made at the beginning of each tow, and the surface water temperature was recorded continuously with a thermograph.

The catch was sorted by species and by age groups when possible. Usually total catches of all species were retained, but occasionally large catches of individual species were subsampled. Discarded fish of a species were weighed as a group and counted or, rarely, their number was estimated on the basis of their average weight in the subsample. Data were taken from some fish on the date of collection, but most specimens were stored in plastic bags in an ice chest and examined on the following day. The data for each tow included counts and total weights of each species and individual total lengths and weights of certain species.

Although this study is based primarily on catches of the "standard" series of bottom trawl tows, information has been used from other bottom trawling, midwater trawls, gill nets, and underwater television. These supplementary data, which were gathered in Lake Michigan (mostly by the R/V *Cisco*) in 1954, 1955, and 1960–67, serve primarily to extend observations into midlevels, into

TABLE 1.—Bottom temperatures at all sampling depths during all standard series of trawl tows in southeastern Lake Michigan

Depth	Distance from shore		Date (1964)										
			Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	Nautical miles	Km.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.
3-----	0.4	0.7	-----	-----	6.7	9.4	14.8	7.9	12.9	22.3	16.5	12.2	11.9
5-----	.6	1.1	0.1	0.4	6.0	9.4	13.8	5.9	10.3	22.1	14.8	12.4	11.9
7-----	.9	1.7	.1	.5	4.0	8.8	13.3	5.4	8.4	16.1	13.4	12.2	11.8
10-----	2.0	3.7	.1	1.2	3.6	6.7	11.9	4.6	5.2	13.5	10.0	12.2	11.7
12-----	2.4	4.5	.2	1.4	3.7	4.3	11.5	4.3	5.0	8.4	7.9	12.2	11.7
15-----	3.3	6.1	.3	1.3	3.3	4.0	8.1	3.9	4.7	6.5	5.7	12.3	11.2
17-----	3.6	6.7	.5	2.0	3.0	3.9	7.8	3.8	4.6	6.4	5.5	11.7	11.0
20-----	4.0	7.4	.7	2.1	2.9	3.5	6.1	3.8	4.3	4.8	4.7	11.7	10.8
25-----	4.9	9.1	1.0	2.1	2.4	3.6	5.1	3.8	4.1	4.8	4.4	11.5	6.1
30-----	5.9	11.0	2.3	2.2	2.2	3.5	4.5	3.5	4.3	4.7	4.4	6.0	5.7
35-----	7.2	13.4	2.2	2.5	2.0	3.2	4.3	3.9	4.1	4.3	4.1	5.0	4.9
40-----	8.9	16.5	2.8	2.7	2.1	3.2	3.9	3.8	3.9	4.2	4.1	4.8	4.8
45-----	13.5	25.1	2.9	2.9	2.2	3.2	3.9	3.9	3.9	4.2	3.9	4.5	4.3
50-----	16.7	31.0	3.1	2.9	2.3	3.0	3.8	3.8	3.9	4.1	4.2	4.5	4.3

bottom areas deeper than those of the standard series, and (to a limited extent) to other portions of the Lake.

Common and scientific names of the species mentioned in the text, listed below, follow the list published by the American Fisheries Society (1960).

Common name	Scientific name
Alewife -----	<i>Alosa pseudoharengus</i>
Gizzard shad -----	<i>Dorosoma cepedianum</i>
Bloater -----	<i>Coregonus hoyi</i>
Shortnose cisco -----	<i>Coregonus reighardi</i>
Longjaw cisco -----	<i>Coregonus alpenae</i>
Kiyi -----	<i>Coregonus kiyi</i>
Lake herring -----	<i>Coregonus artedii</i>
Lake whitefish -----	<i>Coregonus clupeaformis</i>
Lake trout -----	<i>Salvelinus namaycush</i>
American smelt -----	<i>Osmerus mordax</i>
Spottail shiner -----	<i>Notropis hudsonius</i>
Emerald shiner -----	<i>Notropis atherinoides</i>
Carp -----	<i>Cyprinus carpio</i>
Quillback -----	<i>Carpiodes cyprinus</i>
White sucker -----	<i>Catostomus commersoni</i>
Burbot -----	<i>Lota lota</i>
Ninespine stickleback -----	<i>Pungitius pungitius</i>
Trout-perch -----	<i>Percopsis omiscomaycus</i>
Yellow perch -----	<i>Perca flavescens</i>
Johnny darter -----	<i>Etheostoma nigrum</i>
Logperch -----	<i>Percina caprodes</i>
Slimy sculpin -----	<i>Cottus cognatus</i>
Spoonhead sculpin --	<i>Cottus ricei</i>
Fourhorn sculpin ----	<i>Myoxocephalus quadri-</i> <i>cornis</i>

THERMAL CHANGES

The Lake was vertically homothermous at all sampling stations on February 13 and March 11. Bottom temperatures close to shore were near freezing (0.1° C.) and increased with depth to near 3.0° C. at 50 fathoms (table 1). Homothermous conditions continued through early May except near shore. On May 26 bottom temperatures had risen to 14.8 and 11.5° C. at 3 and 12 fathoms, respectively, and some thermal stratification had developed at depths greater than 12 fathoms. From mid-June until late August bottom temperatures of water 15 fathoms and deeper remained cold (3.9–6.5° C.), and thermal stratification became more pronounced. In water shallower than 15

fathoms (and especially at depths less than 12 fathoms) bottom temperatures in summer fluctuated and varied widely (7.9–22.3° C. at 3 fathoms). By October 15 the epilimnion had cooled and thickened so that the water was near 12° C. from surface to bottom at all stations out to 25 fathoms. Cooling progressed little from October 15 to November 4 because of unseasonably warm weather. A detailed account of seasonal thermal changes in Lake Michigan has been published by Church (1942, 1945).

DEPTH DISTRIBUTION

ALEWIFE

Alewives are the most widely distributed of any species in Lake Michigan. Depending on the time of year and life stage, they occupy all depths along the bottom and all waters above the bottom. Vertical distribution is discussed first, in general terms, then bottom distribution is described in more detail.

Young-of-the-year alewives, which hatch mostly in June and July, live at midlevels until late summer or early fall. They have been observed near the surface in early September in midlake and probably occur from shore to shore. They are always caught on the bottom in large numbers by October and have been taken in bottom trawls off Saugatuck as early as August 31. Many, however, are probably at midlevels even in the fall. Nearly all of the young on the bottom, regardless of date of capture, have been 1.5 to 3.5 inches (3.8–8.9 cm.) long, compared with an average calculated 1st-year growth of 3.7 inches (9.4 cm.). Thus, it appears that young alewives are on the bottom only at a certain size, and because the spawning season is rather long, all are not on the bottom at the same time. Possibly some alewives, particularly those which move into midlake in their earlier stages, may not go to the bottom at all in their first year. High winds and resultant turbulent conditions in the fall apparently cause most of the young on the bottom to ascend to midlevels temporarily.

Alewives after their first year tend more strongly toward a bottom existence as they grow older. Yearling alewives (age-group I) are essentially pelagic, but occasionally substantial numbers are on the bottom in the spring and fall, and a few

are usually there in the summer.¹ Alewives move to the bottom in increasing numbers throughout their third year (age-group II) and make up a sizable portion of the bottom catch by late summer. Fish older than 3 years may be found on the bottom at all times, but usually are also at midlevels in varying proportions, depending on the season.

The midwater distribution of alewives, especially when the Lake is homothermous, is poorly known. When the Lake is stratified, young of the year apparently are confined to the epilimnion except in the fall. Concentrations of older fish have been found in the thermocline. Many, especially those older than yearlings, are also regularly above the thermocline and at times are probably present in large numbers a few fathoms off the bottom in areas where the bottom water is warm. In mid-August 1965, alewives older than 1 year were found in midwater from shore to shore in southern Lake Michigan.

The following discussion of bottom distribution is based almost entirely on alewives caught in standard series. Young of the year are referred to as "young" and older fish arbitrarily as "adults."

Young

Young alewives were first caught in the standard series on October 14 (table 2). At that time they were at all bottom depths to 25 fathoms at temperatures of 11.5 to 12.4° C. The temperature at the shallowest depth at which they were absent (30 fathoms) was 6.0° C. On November 4, when the cold bottom water (6.1° C.) had moved shoreward to 25 fathoms, young alewives were taken only at depths of 20 fathoms and less in bottom temperatures of 10.8 to 11.9° C. Largest catches, however, were deeper in November than in October; apparently a movement away from shore was in progress, but fish in the deepest water had moved shoreward to avoid cold water.

Young alewives in the November series were larger in deeper water. The average length ranged from 2.0 to 2.2 inches (5.1 to 5.6 cm.) in the tows at 3 to 10 fathoms and 2.6 to 2.9 inches (6.6 to 7.4 cm.) at 12 to 20 fathoms. This size-depth relation was not apparent in the October series, but was

¹ Large numbers of yearling alewives were concentrated between the breakwalls at the mouth of the Kalamazoo River at Saugatuck in early July 1967. Commercial fishermen, who trawl for adult alewives between breakwalls in the spring and early summer, reported that such large numbers of small ones had not appeared before.

TABLE 2.—Numbers of young-of-the-year (0 group) alewives and young-of-the-year smelt taken in 10-minute trawl tows at various depths, October 14 and November 4, 1964

[No young-of-the-year alewives or smelt were caught at 30, 35, 40, 45, and 50 fathoms on either date; none were taken in standard series on Feb. 13, Mar. 11, Apr. 15, May 5, May 26, June 16, July 7, July 28, and Aug. 21]

Depth	Alewives		American smelt	
	Oct. 14	Nov. 4	Oct. 14	Nov. 4
Fathoms	Number	Number	Number	Number
3-----	6, 658	1, 714	0	0
5-----	2, 985	1, 478	0	0
7-----	1, 701	2, 599	10	0
10-----	312	107	313	564
12-----	780	319	673	247
15-----	525	1, 591	145	89
17-----	75	1, 989	85	37
20-----	602	5, 863	47	3
25-----	302	0	14	0

pronounced in sampling off several ports in southeastern Lake Michigan in 1967.

Adults

Adult alewives showed a more striking seasonal migration than any other species. In February they were concentrated in deep water (table 3). They were taken at 30 to 50 fathoms in the standard series of February 13. The catches increased sharply with depth; 74 were caught at 30 fathoms and 11,267 at 50 fathoms. (Other catches by the R/V *Kaho* and reports from commercial fishermen indicate that concentrations in winter may extend at least to 70 fathoms.) By March 11 the beginning of a shoreward movement was evident. A few alewives were as shallow as 15 fathoms, but concentrations were still at the greatest depths. Movement toward shore was rapid after March 11; by April 15 the largest concentration was at 10 fathoms, and relatively few were taken at depths greater than 17 fathoms. The shoreward movement was probably greatest in the latter portion of the March 11 to April 15 period. Commercial fishermen reported heavy concentrations of alewives at 35 fathoms on April 7; on April 11 the R/V *Cisco* took few at 35 fathoms but large numbers at 20 fathoms. Adult alewives were present in large numbers at 3 fathoms on May 5 and 26. Concentrations probably extended into still shallower water. Catches also were large at 12 and 15 fathoms on May 5 and at 15 to 20 fathoms on May 26. Most alewives on the bottom remained in shallow water throughout the

TABLE 3.—Number of adult alewives (I group and older) taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	Number (¹)	Number (¹)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3-----			938	3, 172	3, 506	466	736	0	90	88	9
5-----	0	0	594	652	917	107	126	11	63	144	176
7-----	0	0	1, 589	531	234	10	505	296	209	36	28
10-----	0	0	4, 201	372	998	38	0	358	208	104	198
12-----	0	0	1, 841	1, 113	708	57	0	162	188	115	238
15-----	0	5	1, 330	1, 019	1, 089	49	1	18	17	346	308
17-----	0	9	636	173	1, 125	40	1	7	8	327	204
20-----	0	28	192	74	1, 416	61	0	0	1	164	396
25-----	0	42	13	26	686	40	0	5	0	224	106
30-----	74	88	13	56	12	6	0	0	0	32	34
35-----	614	824	42	5	2	4	0	0	0	67	52
40-----	3, 326	5, 083	15	0	0	5	0	1	0	8	56
45-----	6, 201	9, 524	85	1	4	0	0	0	0	42	49
50-----	11, 267	7, 494	12	1	0	0	0	0	0	25	28

¹ No data.

summer. Some shift away from shore was evident in late July and August, however, and adult alewives were taken at all sampling depths on October 14 and November 4. Greatest numbers in the fall were at 5 to 25 fathoms.

Catches were considerably smaller in summer and fall than those made earlier. Several factors could account for this decline. In early summer large numbers had moved into the rivers for spawning and many others probably were along the Lake shore in water shallower than 3 fathoms. A substantial die-off in late spring and summer may have reduced the population enough to affect the trawl catches. It is possible also that the larger alewives at midlevels in summer represented a major segment of those which had moved back out into the Lake after spawning. These fish might well have remained at midlevels in the fall.

The size-depth relation of adult alewives changed with the seasons. Larger fish led the migration to shore during late winter and early spring. In February the average lengths at 30, 40, and 50 fathoms were 6.9, 6.6, and 5.5 inches (17.5, 16.8, and 14.0 cm.), respectively; in March at 20, 30, 40, and 50 fathoms the lengths were 7.0, 7.0, 6.6, and 5.9 (17.8, 17.8, 16.8, and 14.0 cm.). Size did not change with depth in April and early May, but after that the average size increased with depth (except in early July, when alewives were concen-

trated close to shore). The unweighted average length of alewives caught in the shallowest and deepest tows of the seven standard series after May 5 was 6.0 inches in the shallowest tows and 6.8 inches in the deepest (only tows that took 10 or more alewives were included).

The seasonal migration of adult alewives observed by Graham (1956) in the Port Credit and Bay of Quinte areas of Lake Ontario closely resembled that in Lake Michigan. Adults began to move from deep water toward shore in April, and numbers were greatest inshore in about middle or late June. Soon after spawning (mostly mid-June to early July) they began to move into deeper water. They appeared in numbers in deep water (25–50 fathoms) about mid-September and were abundant there from December through March.

BLOATER

Bloaters live at midlevels in Lake Michigan until their third year. Few less than 7 inches (17.8 cm.) long are on the bottom. The larvae are in the hypolimnion in deep water (Wells, 1966), but the exact distribution of juveniles at middepths is unknown. The few that have been caught were taken in the thermocline or in upper levels when the water was cool. A few adult bloaters (2 years old or older) are frequently taken at midlevels, almost invariably in or below the thermocline, but the propor-

tion off the bottom is usually small (largest catches in gill nets set obliquely from the surface to the bottom are characteristically near the bottom).

Bloaters on the bottom inhabit intermediate and deep areas, but are sometimes in shallow water. In February, March, and April the largest numbers taken in the standard series were at 25 fathoms and deeper; few were caught during this period at depths less than 20 fathoms, and none were taken in less than 12 fathoms (table 4). A shoreward movement began in May, and by July the greatest numbers were at depths shallower than 20 fathoms. Bloaters avoided warm inshore water, but in the July 7 series, when the inshore water was cooled during an upwelling, the largest catches were at 5 to 12 fathoms and two bloaters were taken at 3 fathoms. Movement into deeper water was pronounced in the fall. On October 14 and November 4 few bloaters were shallower than 17 and 20 fathoms, respectively, and the largest catches were at 35 fathoms.

The above discussion based on the catches of the standard series is, of course, limited to seasonal distribution at depths of 50 fathoms and less. Other experimental fishing indicates that the number of bloaters decreases progressively at depths beyond 50 fathoms. Numbers are occasionally substantial at 60 fathoms but not often at 70 fathoms or deeper. A few bloaters, however, are present in the deepest portion of the southern basin (90

fathoms) and at depths of at least 140 fathoms in the northern basin. (One bloater was taken at 200 fathoms in a gill net fished from the R/V *Cisco* in Lake Superior in 1953.)

The length of bloaters varied little with depth and season. Bloaters in the three shallowest depths at which they were caught in each series, however, usually averaged about 0.2 to 0.4 inch (0.5–1.0 cm.) longer than those in deeper tows. The average length of all bloaters was 8.4 inches (21.3 cm.); 97.1 percent were between 7.0 and 9.9 inches (17.8–25.1 cm.).

Jobs (1949) reported the greatest abundance of bloaters in Lake Michigan at 20 to 59 fathoms. He suspected a movement toward shore in summer and a return to deeper water in fall.

Distribution of bloaters in southeastern Lake Michigan is shallower than in the Apostle Islands region of Lake Superior where largest numbers were usually taken at 40 to 59 fathoms (Dryer, 1966). The shoreward movement in summer and fall in Lake Superior was later and less pronounced than that in Lake Michigan. None were taken at depths less than 10 fathoms, and catches at 10–29 fathoms were never greater than at 40–49 fathoms.

AMERICAN SMELT

American smelt in Lake Michigan move in increasing numbers from a pelagic to a bottom exist-

TABLE 4.—Number of bloaters taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	Number (¹)	Number (¹)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3-----			0	0	0	0	2	0	0	0	0
5-----	0	0	0	1	0	8	177	0	0	0	0
7-----	0	0	0	1	0	59	301	1	3	0	0
10-----	0	0	0	4	0	198	164	14	188	1	1
12-----	0	0	1	12	3	170	119	178	146	4	1
15-----	0	6	0	23	53	144	80	172	137	8	11
17-----	2	9	5	31	95	134	57	207	226	95	12
20-----	13	25	31	39	80	124	59	72	162	75	47
25-----	58	94	71	74	16	102	53	62	98	95	33
30-----	158	63	57	77	30	39	59	66	148	208	94
35-----	145	165	172	63	36	87	47	65	169	391	131
40-----	92	483	300	150	62	148	64	39	89	121	68
45-----	35	132	77	71	46	38	67	58	56	84	77
50-----	98	126	151	103	81	66	53	27	12	33	68

¹ No data.

ence as they grow older. First-year fish (0 group) live in the upper levels until the fall (or very late summer) when at least some move to the bottom. In their second year (I group) they may be either at midlevels (commonly in the thermocline) or on the bottom. After their second year (II group and older) they are mostly on the bottom. Ferguson (1965) reported a diurnal vertical migration of adult smelt in eastern Lake Erie. In the discussion below "young" refers to young of the year and "adults" (arbitrarily) to older fish.

Young

Appreciable numbers of young smelt were caught in the trawls on October 14 and November 4, mostly at 10 to 15 fathoms (table 2). No change in distribution appeared between the two periods. None had been taken prior to October 14, but the nearly 2-month span since the immediately preceding series on August 21 precludes a statement of the exact time they first appear on the bottom. Most young smelt in the Apostle Islands region of Lake Superior were caught at less than 10 fathoms and seldom were deeper than 19 fathoms (Dryer, 1966). In eastern Lake Erie they frequented the shallow epilimnial waters and at times were highly concentrated near shore (Ferguson, 1965).

Adults

Adult smelt on the bottom occupy shallow and intermediate depths in southeastern Lake Michigan. They were caught consistently during stand-

ard series but never in large numbers (table 5). They were widely scattered from 7 to 35 fathoms on February 13, but most had abandoned the deeper water by March 11, when greatest numbers were at 10 to 17 fathoms. Most older smelt had moved into very shallow spawning areas by April 15, when few were caught. Smelt reappeared in the catches on May 5, at depths of 3 to 10 fathoms. They had extended their range to 20 fathoms by May 26. Thereafter none were taken deeper than 20 fathoms but they avoided warm water near shore.

The length of smelt varied with depth. In spring and summer (except during the spawning season) those in shallow water were largely yearlings (which averaged 3.2 inches or 8.1 cm.) and those in deeper water were mainly older fish (average 5.3 inches or 13.5 cm.). In the fall, yearlings and older fish could not be separated readily by size, but the larger fish still preferred deeper water. The average length on November 4 was 5.4 inches (13.7 cm.) at 5 to 7 fathoms and 6.8 inches (17.3 cm.) at 10 to 20 fathoms.

Adult smelt in northern Lake Michigan, where they are far more abundant than in the southeastern portion of the Lake, extend their summer range into deeper water than in southeastern Lake Michigan. They were commonly taken in the northern area by the R/V *Cisco* in 1961 at 25 to 35 fathoms and occasionally in small numbers at 50 fathoms. The largest catches were at 15 fathoms (usually the shallowest water fished).

TABLE 5.—Number of adult American smelt taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms ¹	Number (²)	Number (²)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3			0	2	0	10	0	0	0	0	0
5	0	0	2	54	0	7	33	0	0	0	3
7	2	1	0	44	4	7	12	0	17	0	8
10	1	6	0	16	6	11	4	11	0	3	5
12	2	6	0	0	14	7	0	2	2	8	1
14	1	10	0	0	17	2	0	4	3	6	6
17	1	9	0	0	11	1	1	0	1	5	6
20	1	0	0	0	1	0	1	1	0	0	5
25	5	1	0	0	0	0	0	0	0	0	0
30	3	0	0	0	0	0	0	0	0	0	0
35	1	0	0	0	0	0	0	0	0	0	0

¹ No adult smelt were caught deeper than 35 fathoms.

² No data.

Most yearling (I group) smelt in the Apostle Islands region of Lake Superior were caught at less than 10 fathoms, and older ones were most common at 10 to 39 fathoms (Dryer, 1966).

SPOTTAIL SHINER

The spottail shiner was more strongly limited to shallow water than other common species; it was the only species caught in the shallowest tows of every series (table 6). The range was extended into intermediate depths, however, in winter and fall. Shiners were irregularly distributed from the shallowest depths to 20 or 25 fathoms in February–April; numbers were greatest at 3 to 17 fathoms. A definite shoreward movement was evident by May 5. None were caught deeper than 7 fathoms from May 26 to August 21. For each of the six series in May to August the average percentages of the total catch that were taken at 3, 5, and 7 fathoms were 42.5, 48.2, and 9.3 percent, respectively. In other years, however, spottail shiners have occurred in appreciable numbers as deep as 12 fathoms in summer, when very warm water extended on the bottom to that depth. Catches in shore seines near the trawling area indicated that they also may be common at depths less than 3 fathoms. By October 14 spottail shiners had scattered into water as deep as 17 fathoms; largest catches were at 12 and 15 fathoms. They were caught at depths of 3 to 15 fathoms on November 4, except for one taken at 25 fathoms; largest numbers were at 5 fathoms, but all catches were small.

Larger spottail shiners tended to be at the deeper

end of the distribution throughout the year. The average weight from tows which contained at least 10 individuals was 0.37 ounce (10.5 g.) in the shallowest tow and 0.51 ounce (14.5 g.) from the deepest (unweighted mean of average for each series). Spottail shiners taken on October 14 averaged 4.0, 4.4, and 4.7 inches (10.2, 11.2, and 11.9 cm.) at 10, 12, and 17 fathoms, respectively.

TROUT-PERCH

Trout-perch were restricted to shallow and intermediate depths. Most fish in the small catches of February–April were at 12 to 17 fathoms, but they were scattered from 5 to 30 fathoms (table 7). Trout-perch were concentrated nearer shore in May, when most were at 5 and 7 fathoms, and none were caught deeper than 17 fathoms. The depth of greatest abundance of trout-perch continued to be 5 to 7 fathoms in summer, and the maximum depth at which they were taken was only 10 fathoms. In the summer of other years, however, they have been caught in appreciable numbers as deep as 15 fathoms when epilimnial waters reached the bottom at that depth. Trout-perch had moved back into deeper water by October 14, when they were at 10 to 20 fathoms, and largest numbers were at 12 fathoms. On November 4 a few trout-perch were caught at 3 and 5 fathoms, but most were at 10 to 20 fathoms.

Average weights of trout-perch in each catch suggest some segregation by size, but no clear-cut size-depth relation.

TABLE 6.—Number of spottail shiners taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms ¹	Number (²)	Number (²)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3-----	11	45	16	88	44	70	626	2	62	4	18
5-----	12	11	5	1,046	299	11	15	80	421	5	24
7-----	21	28	22	3	0	0	0	0	25	0	1
10-----	33	39	39	0	0	0	0	0	0	12	1
12-----	82	19	24	0	0	0	0	0	0	75	2
15-----	13	30	4	3	0	0	0	0	0	74	3
17-----	1	8	1	0	0	0	0	0	0	7	0
20-----	0	1	0	0	0	0	0	0	0	0	0
25-----											1

¹ No spottail shiners were caught deeper than 25 fathoms.

² No data.

TABLE 7.—Number of trout-perch taken in 10-minute trawl tows at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms ¹	Number (²)	Number (²)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3			0	6	0	46	16	0	18	0	2
5	1	0	1	134	117	74	186	0	648	0	1
7	0	0	3	31	185	39	2	11	18	0	0
10	4	5	5	2	8	1	0	22	1	12	7
12	3	15	6	1	28	0	0	0	0	44	3
15	12	15	10	1	2	0	0	0	0	4	2
17	12	9	9	2	2	0	0	0	0	3	14
20	9	3	2	0	0	0	0	0	0	2	6
25	2	1	4	0	0	0	0	0	0	0	0
30	1	1	1	0	0	0	0	0	0	0	0

¹ No trout-perch were caught deeper than 30 fathoms.² No data.

Dryer (1966) reported that trout-perch in the Apostle Islands region of Lake Superior were widely distributed down to 49 fathoms, were most abundant at 10 to 19 and 30 to 39 fathoms, and exhibited no seasonal changes in distribution.

YELLOW PERCH

Yellow perch in their first 2 years of life in southeastern Lake Michigan are in water shallower than 3 fathoms, as indicated by their presence in shore seines and scarcity in trawls fished as shallow as 3 fathoms. No young-of-the-year (O group) yellow perch and only 23 yearlings (I group), distinguished by size, were caught in the 11 standard series. Extensive trawling off Grand Haven, Mich. (23 nautical miles north of Saugatuck), in 1954 and 1960 produced only one large catch of young-of-the-year perch (4 fathoms, November 20, 1954) and two of yearlings (5 and 7 fathoms, June 20, 1960). The yearlings were caught during a mild upwelling. The depth distribution of small yellow perch in southeastern Lake Michigan contrasts strikingly with that in Lake Erie, where research vessels of the Bureau of Commercial Fisheries regularly have found large numbers of young of the year (as small as 1.2 inches or 3.0 cm.) in depths to 6 fathoms and yearlings commonly to 17 fathoms. Young-of-the-year perch in Saginaw Bay (Lake Huron) strongly preferred water shallower than 2 fathoms in summer, but many moved several fathoms deeper in October (R/V *Cisco* trawling and shore-seining records, 1956). Year-

lings were distributed at least as deep as 7 fathoms in summer.

Adult yellow perch (defined here as those older than 2 years) in southeastern Lake Michigan inhabit shallow and intermediate depths. Most are on the bottom, but appreciable numbers may be at midlevels in summer. Greatest numbers in February to early May were at 10 to 12 fathoms, and the extreme depth range was 5 to 25 fathoms (table 8). A movement into shallower water was in progress by May 26. Yellow perch congregate in middle and late May for spawning at depths less than 8 fathoms on rocky bottom about 2 miles south of the trawling area. Most adult yellow perch were at 7 fathoms or less during summer. Substantial numbers probably were often shallower than 3 fathoms; the maximum depth was 10 to 12 fathoms. Perch have been abundant as deep as 12 to 17 fathoms during occasional periods in August of other years when warm water reached unusual depths. Adult yellow perch moved into deeper water in fall. None were taken at depths shallower than 10 fathoms in the October 14 and November 4 standard series. The largest catch on November 4 was at 20 fathoms, but no fish were caught deeper. The fall movement of yellow perch into greater depths in Lake Michigan can be more pronounced than the catches of the standard series indicate. An extremely heavy catch was made off Charlevoix, Mich., on October 17, 1955 in a gill net at 25 fathoms (bottom temperature 15.1° C.), where none had been taken in several sets in spring and summer.

TABLE 8.—Number of yellow perch, II group and older, taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms ¹	Number (²)	Number (²)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3			0	0	24	138	1,082	240	108	0	0
5	18	76	0	28	48	114	46	978	157	0	0
7	14	9	8	23	85	240	110	6	72	0	0
10	70	28	55	422	22	7	2	25	1	7	3
12	42	194	35	46	16	0	0	22	0	27	23
15	29	26	16	5	2	0	0	0	0	35	9
17	4	12	0	1	0	0	0	0	0	5	3
20	0	4	0	0	1	0	0	0	0	2	53
25	0	0	0	1	0	0	0	0	0	1	0

¹ No yellow perch caught deeper than 25 fathoms.

² No data.

In the summer, appreciable numbers of yellow perch follow warm upper strata farther out into the Lake than their normal range on the bottom. They have been taken on several occasions from the upper portions of gill nets set obliquely from top to bottom at a bottom depth of 26.7 fathoms along the eastern shore of Lake Michigan. About 90 percent were from the epilimnion (usually about the upper 10 fathoms); all were from the upper 17 fathoms.

Yellow perch, usually in poor condition, occasionally have been taken on the bottom at great depths in Lake Michigan. The deepest recorded by the R/V *Cisco* was a fish taken at 140 fathoms off Frankfort, Mich. (June 29, 1955); another was caught at 100 fathoms in Grand Traverse Bay (June 3, 1955).

Size of adult yellow perch varied somewhat with depth. Larger ones were inclined to be in shallower water in February, March, and April; among tows in which at least 10 perch were taken the average length was 8.8 inches (22.4 cm.) for the shallowest tow and 7.7 inches (19.6 cm.) for the deepest (unweighted means of averages for each of the three series). The size-depth relation was reversed in May to August when average lengths for fish from the shallowest and deepest tows were 7.2 and 8.0 inches (18.3 and 20.3 cm.), respectively. Size did not change with depth in the fall.

SLIMY SCULPIN

Larval slimy sculpins are at midlevels, mostly in the hypolimnion. Little else is known of the O

group, except that some apparently appear on the bottom in the fall. Most slimy sculpins caught in the standard series were between 2 and 4 inches (5.1 and 10.2 cm.) long and probably included yearlings and older fish. In the series of November 4, however, the catches at 25 and 30 fathoms contained 72 and 5 individuals, respectively, between 1.0 and 1.5 inches (2.5 and 3.8 cm.) long. Studies of age and growth by Rottiers² suggest that these fish were young of the year. They are not included in the following discussion.

The depth range of slimy sculpins extends beyond the maximum depth of the present standard series of collections. Limited trawling data for greater depths indicate that in summer slimy sculpins are present in small numbers at least to 71 fathoms but are rare or absent at 85 fathoms. Deason (1939) found them in stomachs of lake trout and burbot caught in Lake Michigan as deep as 70 fathoms, but concluded that they were usually between the shore and 50 fathoms.

The slimy sculpin is distributed over a wide depth range in winter, but abandons shallow areas in spring as soon as warming is significant and continues a gradual movement away from shore through summer and fall. Greatest numbers of slimy sculpins on February 13 were at 10 to 35 fathoms (table 9). They were in all catches except at 45 and 50 fathoms (where an occasional specimen might have been overlooked because of the

² Rottiers, Donald V. Some aspects of the life history of *Cottus cognatus* in Lake Michigan. Master's thesis, University of Michigan, 1965, 49 pp.

TABLE 9.—Number of slimy sculpins taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms	Number (¹)	Number (¹)	Number	Number	Number	Number	Number	Number	Number	Number	Number
3-----			14	0	0	0	0	0	0	0	0
5-----	10	2	15	4	0	0	0	0	0	0	0
7-----	5	10	43	8	0	1	0	0	0	0	0
10-----	51	22	97	4	0	5	0	0	0	0	0
12-----	109	61	90	6	2	4	0	0	0	0	0
15-----	117	118	115	44	2	29	37	1	0	1	2
17-----	107	121	91	161	19	36	72	0	4	0	1
20-----	117	97	122	48	54	101	100	41	44	3	1
25-----	106	146	35	32	187	122	133	132	124	58	68
30-----	171	293	42	11	138	170	100	88	97	73	139
35-----	74	126	14	60	75	65	86	75	86	81	97
40-----	9	43	9	38	41	46	139	79	119	105	140
45-----	0	28	29	41	46	31	42	36	66	14	36
50-----	0	6	8	46	38	21	29	31	12	15	15

¹ No data.

great quantities of alewives). Small numbers appeared in the catches at 45 and 50 fathoms on March 15, but distribution had not changed significantly. In every later series, slimy sculpins were found at all depths greater than 17 fathoms. A slight shift shoreward was evident on April 15, when greatest numbers were at 7 to 30 fathoms. They had started to move away from shallow water by May 5, when relatively few were at 12 fathoms or shallower, and none were at 3 fathoms. A general trend away from shore continued thereafter until fall. On May 26 the shallowest depth of capture was 12 fathoms, and on August 21 it was 17 fathoms; largest numbers in the period May 26–August 21 were at 20 to 40 fathoms. On October 14 and November 4 most were at 25 to 40 fathoms, and few were at 20 fathoms or shallower.

Slimy sculpins beyond the earlier growth stages ordinarily are considered strict bottom dwellers, but at times larger ones may ascend several fathoms above the bottom in Lake Michigan. On May 20, 1955, 20 (probably slimy sculpins, but possibly spoonhead sculpins) were caught at night (about 2000 e.s.t.) in a trawl fished by the R/V *Clisco* 6 fathoms above the bottom where total depth was 23 fathoms; another was taken at night on November 18, 1954, 27 fathoms above the bottom at a 40-fathom depth. On June 20, 1967, 31 slimy sculpins were caught during daytime by the Bureau's R/V *Nisicowet* 3 to 9 fathoms above the bottom in turbid

water 13 to 14 fathoms deep in western Lake Superior (Merryll Bailey, personal communication).

Slimy sculpins were concentrated in deeper water in the Apostle Islands region of Lake Superior than in southeastern Lake Michigan; they were most common in the Apostle Islands at depths greater than 40 fathoms, and probably the greatest numbers were at 50 to 59 fathoms (Dryer, 1966).

The depth distribution of slimy sculpins in southeastern Lake Michigan varied noticeably with size in winter and early spring, but not thereafter. Sculpins at intermediate depths were smaller than at other depths in February to May. In the five series of February 13 to May 26, the average weights of sculpins taken at depths less than 30 fathoms were 0.36, 0.34, 0.32, 0.24, and 0.23 ounce (10.2, 9.6, 9.1, 6.8, and 6.5 g.) respectively; at 30 to 40 fathoms the averages were 0.27, 0.27, 0.14, 0.12, and 0.16 ounce (7.7, 7.7, 4.0, 3.4, and 4.5 g.); and at 45 and 50 fathoms (no data for February 13 and March 11) the weights were 0.30, 0.21, and 0.25 ounce (8.5, 6.0, and 7.1 g.). No obvious size-depth relation existed after May, but some tendency existed for the larger fish to be in intermediate depths in August–November—the opposite of the situation in early season.

FOURHORN SCULPIN

Fourhorn sculpins (also called deepwater sculpins) are confined to deep water much more than

any of the other species. They were uncommon in the catches shallower than 40 fathoms in the standard series. Data from additional trawling of the R/V's *Cisco* and *Kaho* indicate that fourhorn sculpins are present in the deepest part of the southern basin (90 fathoms) and are abundant to at least 70 fathoms. They are found at least as deep as 140 fathoms in northern Lake Michigan, where their range does not appear to extend into as shallow water as in the southern basin. Deason (1939) estimated the depth of greatest abundance of fourhorn sculpins in Lake Michigan as 40 to 75 fathoms on the basis of their occurrence in stomachs of lake trout and burbot. Fourhorn sculpins in the Apostle Islands region of Lake Superior were seldom shallower than 50 fathoms (Dryer, 1966); they were fairly abundant in R/V *Cisco* trawl catches at 200 fathoms in eastern Lake Superior in 1953.

Larval fourhorn sculpins are in the hypolimnion in deep areas. No other information is available on distribution in the first year.

Although the standard series did not cover a large enough portion of the depth range of fourhorn sculpins to give a good indication of seasonal distribution, certain features are evident from the data. The species was always abundant at 45 and 50 fathoms, but was never numerous at other depths (table 10). It extended its range slightly shoreward in spring. None were shallower than 45 fathoms on February 13, but a few were as shallow as 35 fathoms on March 11 and 17 fathoms on April 15. Numbers which had been considerably larger at 50 fathoms than at 45 fathoms in February-May were usually larger at 45 fathoms afterwards. Distribution showed no obvious change in summer and fall.

The shallowest water in which a fourhorn sculpin was caught in the standard series was 7 fathoms (May 26), but one specimen, seemingly in good condition, was taken at 4 fathoms off Saugatuck in August 1965.

The segment of the depth range of fourhorn sculpins sampled in the standard series was too small for an evaluation of the size-depth relation. The average individual weight in most catches was 0.8 to 1.0 ounce (22.7-28.3 g.). Fourhorn sculpins in the standard series were not measured, but 80 percent of those from identical trawling off Saugatuck in 1965 were 4.5 to 5.5 inches (11.4-14.0 cm.) long, and few fell outside the length range 4.0 to 6.0 inches (10.2-15.2 cm.).

OTHER SPECIES

Several species were caught in such small numbers in the standard series that their depth distribution could not be determined accurately. The limited data available are discussed briefly.

Shortnose ciscoes (18 collected) were taken at 5 to 50 fathoms, mostly 40 to 50 fathoms. One long-jaw cisco was caught at 15 and another at 50 fathoms, and individual kiyis were taken at 45 and 50 fathoms. Lake herring (62 collected) were taken at 5 to 50 fathoms; they were most common at 15 to 25 fathoms, especially on February 13 and March 11. In the mid-1950's, when this species was more abundant in Lake Michigan, it was frequently caught in nets of the R/V *Cisco* at mid-levels, occasionally near the surface. Studies by Smith (1956) and Dryer (1966) indicated that lake herring in the Great Lakes are essentially pelagic during the warm months, but may be

TABLE 10.—Number of fourhorn sculpins taken per 10-minute trawl tow at various depths, February 13 to November 4, 1964

Depth	Date										
	Feb. 13	Mar. 11	Apr. 15	May 5	May 26	June 16	July 7	July 28	Aug. 21	Oct. 14	Nov. 4
Fathoms ¹	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number
17-----	0	0	1	0	0	0	0	0	0	0	0
20-----	0	0	1	0	0	0	1	0	1	0	0
25-----	0	0	1	0	0	0	1	0	0	0	0
30-----	0	0	2	2	1	2	1	0	1	1	1
35-----	0	7	2	3	4	3	3	3	4	3	0
40-----	0	22	13	35	25	13	22	12	30	38	25
45-----	105	85	235	303	356	324	494	264	732	454	228
50-----	279	876	580	508	500	289	425	381	275	286	250

¹ No fourhorn sculpins caught at depths shallower than 17 fathoms, except for one at 7 fathoms on May 26.

abundant on the bottom at other times. The ranges of all the ciscoes mentioned here, especially the kiyi, extend into water deeper than 50 fathoms in southeastern Lake Michigan.

Lake whitefish (5 collected) were taken at 3 to 20 fathoms. Seven carp were caught at 5 to 7 fathoms. Ninespine sticklebacks (3 collected) were at depths of 20 to 50 fathoms. This species is more common in bottom catches in most other parts of the Lake and is occasionally taken at midlevels. Johnny darters (19) were collected at 7 to 35 fathoms (mostly 12–17) and logperch (12) at 5 to 12 fathoms. Single individuals of gizzard shad, white sucker, and quillback were caught at 3, 5, and 15 fathoms, respectively.

EFFECTS OF TEMPERATURE ON DISTRIBUTION

Temperature was the most obvious factor in the depth distribution of fish in this study. Even in winter, temperature influenced the distribution of some of the species. Alewives and bloaters, for example, congregate in the deeper areas to avoid the colder inshore waters. Numbers of both species increased significantly at 15 to 20 fathoms between February 13 and March 11 as bottom temperatures rose from 0.3–0.7° C. to 1.3–2.1° C. The movement toward shore in the spring of all species except the sculpins is closely correlated with a warming of inshore waters. The shift of all species except the fourhorn sculpin into deeper water in the fall also is obviously related to temperature. As warm water steadily encroaches on deeper bottom areas warm-water species spread with it, and cold-water forms move deeper to avoid it. The control of temperature over depth distribution is best seen in summer when thermal changes are most pronounced.

After thermal stratification, bottom temperatures in water shallower than 12 or 15 fathoms in southeastern Lake Michigan are seldom stable for any length of time. Direction and speed of wind influence water temperatures strongly. Onshore winds thicken the epilimnion near shore and increase the depth to which warm water extends on the bottom; offshore winds have the opposite effect. Exceptionally strong, persistent northeast or north winds cause extensive upwellings along a large portion of the east shore of the Lake and hypolimnial water of 5 to 6° C. may replace water of 20° C. in

1 or 2 days. At such times cold water from surface to bottom may extend from shore several miles out into the Lake, and no warm bottom water is available to the fish.

Catches of the standard series illustrate the influence of thermal conditions on the depth distribution of fish in summer. A comparison may be made between the catches of July 7, when epilimnial waters near shore were relatively cool and the hypolimnion extended into shallow water, and July 28, when epilimnial waters were much warmer and reached the bottom to greater depths. The thermal conditions of July 28 were more common for summer; those of July 7, though less frequent, were by no means unusual. Species in the shallowest water had a deeper distribution on July 28. Bloaters and slimy sculpins showed changes only in the shallow extremity of their depth range because the temperature in the remainder of their range was unchanged. The fourhorn sculpin was too deep to be affected.

The standard series were too infrequent to show the rapidity of movement in response to temperature change; however, evidence from other trawling indicates that appreciable movement may occur in a few hours, and that major redistribution may take place in 2 or 3 days. On August 24, 1963, tows were made in the morning (0807–1001 e.s.t.) and afternoon (1344–1541 e.s.t.) at 7, 10, and 12 fathoms off Saugatuck during a period of rather rapidly changing bottom temperatures. The temperature remained steady at 16.5° C. at 7 fathoms but rose from 12.6 to 14.0° C. at 10 fathoms and from 12.4 to 13.3° C. at 12 fathoms (table 11). At the same time several species moved into deeper water. Spottail shiners decreased drastically at 7 fathoms and increased greatly at 10; several appeared in the afternoon catch at 12 fathoms where none had been taken in the morning. Catches of yellow perch decreased slightly at 7 fathoms and strongly at 10 fathoms and increased drastically at 12. No other species were present in significant numbers at 7 fathoms in either period. Troutperch decreased appreciably at 10 fathoms and increased correspondingly at 12. Bloaters decreased at both 10 and 12 fathoms. Smelt showed only a slight change at 10 fathoms and none at 12. Alewives did not change significantly. Sculpins were not caught in any of the tows. These changes do not necessarily indicate that individual fish

TABLE 11.—Trawl catches in identical morning (0807–1001 e.s.t.) and afternoon (1344–1541 e.s.t.) tows at various depths off Saugatuck, Mich., August 24, 1963

[Bottom temperatures (° C.) with each tow are in parentheses]

Species	7 fathoms		10 fathoms		12 fathoms	
	a.m. (16.5)	p.m. (16.5)	a.m. (12.6)	p.m. (14.0)	a.m. (12.4)	p.m. (13.3)
	Number	Number	Number	Number	Number	Number
Alewife.....	12	3	39	51	39	34
Bloater.....	0	1	49	23	184	65
American smelt.....	1	3	193	246	92	87
Spottail shiner.....	36	1	5	113	0	5
Trout-perch.....	9	3	254	146	5	92
Yellow perch.....	97	76	233	113	34	246

traveled a great distance (e.g., the 0.5 nautical mile from 10 to 12 fathoms), but may reflect a more modest shift of the entire populations of various species.

A pronounced shift in depth distribution of fish during a few days occurred between August 14 and 17, 1962, when trawl tows were made at 7, 10, 12, and 15 fathoms off Saugatuck. Bottom temperatures in this period rose from 7.9 to 17.7° C. at 7 fathoms and from 5.9 to 11.2° C. at 15 fathoms. Spottail shiners were rare as deep as 7 fathoms at the cooler temperatures on the earlier date, but were common out to 12 fathoms when the water warmed. Trout-perch were caught only at 7 fathoms on August 14, but were concentrated at 15 fathoms on the 17th. Yellow perch, bloaters, and smelt moved similarly. Alewives, which characteristically responded less to sudden temperature changes than other species, showed little movement. Sculpins were not in the catches.

Shifts in the depth distribution of fish in shallow water in summer, although not usually as abrupt as the examples cited, are frequent if not almost continuous in southeastern Lake Michigan (and probably along other exposed shorelines of the Lake as well) as bottom temperatures fluctuate. During upwellings, however, warm-water species may suddenly be exposed to temperatures much colder than those preferred from which they cannot escape. Such conditions can occur at crucial times, such as the spawning season or during hatching. It would seem then that temperatures for these species would be much more suitable in terms of growth rates and spawning success in smaller bodies of water or protected bays, where thermal stability is greater.

TEMPERATURE PREFERENCES

Certain generalities regarding temperature preferences of the various species are possible from the standard series and other trawling at Saugatuck, although unstable thermal conditions and other factors prevented any determination of either exact temperature preferences or "final preference" (see Fry, 1947). These observations apply to adult fish during periods when the range of temperatures on the bottom was wide.

All species except fourhorn sculpins were in water with a temperature range of several degrees. Alewives apparently had the least temperature specificity. At times they were simultaneously in water from 5° C. or less to 20° C. or more, but most were in water warmer than 8° C. Evidence suggests that they tend to shun temperatures greater than 22° C., although in some spawning streams they must occasionally endure temperatures of 25° C. or more. Bloaters generally inhabited water from 4 to 11° C., although a few usually were present at temperatures several degrees higher; greatest concentrations often were at 6 to 10° C. Smelt were mostly in water of intermediate temperatures, about 6 to 14° C. Spottail shiners with few exceptions were in water from 13° C. to the warmest available. Trout-perch were mainly in water of 10 to 16° C. Yellow perch were usually in water above 11° C. and were occasionally abundant in water as warm as 22° C.; substantial numbers, however, were found at temperatures as low as 8° C. Slimy sculpins were seldom taken in water above 10° C., and most were at 4 to 6° C. Occasionally in fall overturns, however, when moderately warm water reached bottom at greater depths,

large numbers of slimy sculpins were taken from water as warm as 13° C. Fourhorn sculpins with rare exceptions were restricted to water colder than 4.5° C. Factors other than temperature must exert a strong influence on the depth distribution of fourhorn sculpins because they did not move into shallow water in numbers even where temperatures were under 4.5° C.

ACKNOWLEDGMENT

E. H. Brown furnished age data for Lake Michigan alewives and bloaters.

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BIOLOGY OF THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN, IN THE ST. JOHNS RIVER, FLORIDA

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ABSTRACT

Blue crabs commonly mated from March to July and from October to December in the St. Johns River; the proportion of males and females that matured at a small size was larger in salt water than in fresh water.

Blue crabs spawned in the first 30 km. of river above the mouth, and the eggs hatched in the ocean within 6 km. of shore. Spawning began as early as February and continued through October.

Some blue crabs of both sexes migrated from the St. Johns River to the Intracoastal Waterway, to four other rivers, and to the ocean. Among crabs tagged 40 to 195 km. above the mouth of the St. Johns River and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured downstream from the point of release. Many females tagged in the ocean were recaptured in inland waters throughout the year. During the spawning

season some reentered the St. Johns River for a second spawning within 15 days after their eggs hatched.

First- and second-stage zoeae and megalops of crabs of the genus *Callinectes* were collected as far as 40 km. upstream. Of 22 kinds of crab zoeae collected near the mouth, *Callinectes* ranked third in abundance in 1961 and second in 1962.

Small blue crabs (2–9 mm. wide) entered the river in waves and moved as far as 135 km. upstream. Nearly all of the upstream migrants were beyond the first post-larval stages except during early winter.

Blue crabs 5 to 200 mm. wide fed principally on mollusks (primarily clams and mussels), fish, and crustaceans (primarily amphipods and crabs). Generally, they ate the same type of food regardless of crab size, area, and season.

This report presents the results of studies in 1961–63, on the biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River. Detailed information on their biology is necessary to learn which factors affect the harvestable population.

The blue crab supports important fisheries along the Atlantic and Gulf coasts of the United States. Landings in 1950–65 averaged about 58 million kg. per year. The 1965 catch was 71 million kg., worth slightly more than \$12 million to the fishermen. In the St. Johns River, 109 fishermen, using pots and 52 fishing trawls, caught 1,465,840 kg. of blue crabs during 1962 (Tagatz, 1965).

The biology of the blue crab has been investigated extensively in Chesapeake Bay (Hay, 1905; Churchill, 1919; Truitt, 1939; Pearson, 1948; and Van Engel, 1958), and to a lesser degree in Delaware (Porter, 1956), Louisiana (Darnell, 1959), and Texas (Daugherty, 1952; Pounds, 1961). No

investigation has been reported, however, of the biology of the blue crab in the St. Johns River or in other Florida waters.

Blue crabs occur far upstream in the St. Johns River, at least as far as Lake Harney, 305 km. above the mouth (Moody, 1963). Their widespread distribution in the fresh-water portion of the river is thought to be largely due to the abundance of calcium chloride in the water and to the presence of the salt springs that drain into the river (Odum, 1953). In other estuaries, blue crabs seldom penetrate far into fresh water (Williams, 1965). Our studies on the St. Johns River extended 215 km. upstream to Astor, the terminus of the commercial fishery for crabs (fig. 1).

MATERIALS AND METHODS

Sampling and tagging were conducted to determine the size, sex composition, sexual maturity, distribution, and movements of adult blue crabs.

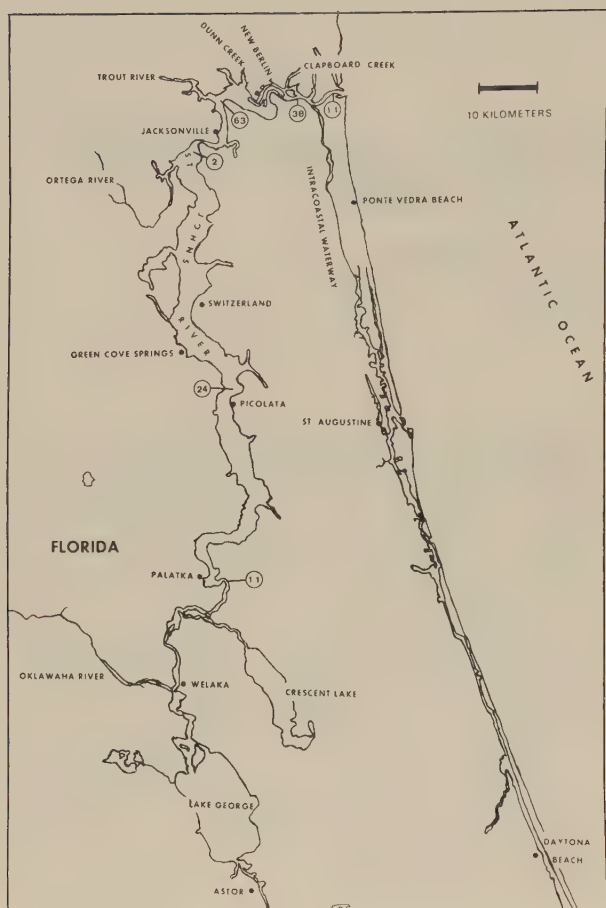


FIGURE 1.—St. Johns River, Fla., from mouth to Astor. (Circled numerals indicate buoys referred to in text.)

In 1961 and 1962, 92 samples of about 150 crabs each were obtained from the uncultured commercial catches of crabs in the river, and on 1 or 2 days each month, crabs were observed in catches of shrimp trawlers fishing 1 to 8 km. offshore between Fernandina Beach and Ponte Vedra Beach. Samples were taken monthly with a 3-m.-wide trawl at selected stations in the river to supplement data from the fishery. Size, recorded as width, is the distance between the tips of the large lateral spines of the carapace.

I examined females and every fifth male crab in samples from commercial catches for sexual maturity, which is more obvious in the female blue crab than in the male—the apron (abdomen) is semicircular in mature females and triangular in immature females. I also examined every fifth mature female to determine stage of ova development. The shape of the apron of the male does not

change at maturity; I based maturity in males on the development of the anterior and middle vasa deferentia. In the mature male the vasa deferentia are large prominent ducts and the middle vas deferens is bright pink. In the immature male the vasa deferentia are small and the middle vas deferens is white.

From April 1961 to April 1963, 8,927 blue crabs (6,383 males, 2,544 females) were tagged in the St. Johns River and 2,595 (58 males, 2,537 females) in the ocean off the mouth of the river, 1.5 to 5 km. offshore and 1.5 km. north to 11 km. south of the jetties. I obtained these crabs from commercial fishermen. Only mature females and males wider than 135 mm. were tagged; maturity of males could not be determined by external observation. Each tag was plastic, bore a number, and was fastened by stainless steel wire between the large lateral spines of the carapace (fig. 2). Cronin (1949) reported that this method of tagging was more effective than others he tested.

I collected larval crabs in the St. Johns River in 1961 and 1962, using Clarke-Bumpus samplers for simultaneous collections at the surface (0.3-m. depth) and bottom (10 m.). Collections, water temperatures, and salinities (surface and bottom) were obtained hourly over any selected 4- to 11-hour period. Captured plankton was placed in jars which were then filled to capacity (135 ml.) by addition of water. Crab larvae were identified and counted in three 4-ml. subsamples removed from each jar.

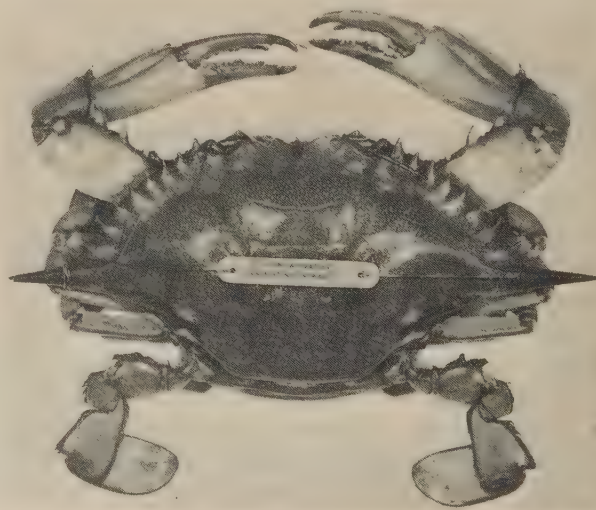


FIGURE 2.—Blue crab with carapace tag attached.

Reliable separation of the larvae of *Callinectes sapidus* from those of other species of *Callinectes* is not yet possible. Because *C. similis* and *C. ornatus* are common in the lower 40 km. of the river and in the ocean off the river's mouth (Williams, 1966), and their spawning seasons coincide with that of *C. sapidus*, larvae of *Callinectes* were designated by genus only.

A 21-m.-long seine with a funnel-shaped bag (4-mm. stretched mesh) and a 2.5-m.-wide trawl (tail bag was 6-mm. stretched mesh) were used to determine the distribution of juvenile blue crabs in the St. Johns River. In addition to extensive random sampling (1961-63), certain areas were sampled at 2-week intervals (1962-63).

The stomachs of 695 blue crabs 5 to 200 mm. wide were obtained from December 1962 to August 1963 for the food study. Crabs were selected from samples taken during scheduled collecting with a seine and trawl. The percentage frequency of each class of organism was determined. For each stomach, the percentage of each food type in the total volume of food was estimated.

Aquatic plants, fish, and invertebrates obtained in the nets and with a Petersen dredge were counted to indicate natural abundance of foods selected by crabs, and representative specimens were preserved for comparison with stomach contents.

THE ST. JOHNS RIVER

The St. Johns River lies entirely within Florida. It rises from headwater marshes 80 km. north of Lake Okeechobee and 24 km. inland from Florida's east coast, flows north for 420 km. to Jacksonville, and continues east 40 km. to the Atlantic Ocean. North and south jetties extend from the mouth of the river about 1.5 km. into the ocean. Along its course the river receives the flow of many tributaries and often expands into lakes. Its largest tributary is the 200-km.-long Oklawaha River (172 km. upstream); its largest lake is 9.5-km. wide and 19-km. long Lake George (185 km. upstream). The Intracoastal Waterway intersects the river 8 km. from the mouth. The St. Johns River is less than 1.5 km. wide from the jetties to 11 km. upstream, 1.5 to 5 km. wide from this point 125 km. upstream to Palatka (except for a narrow section at Jacksonville), and 1.5 km. wide from Palatka upstream 145 km. to Sanford. Upstream

from Sanford, the greatest width is less than 1 km. The depth of the river channel is 10 m. from the mouth to Jacksonville, 4 m. to Palatka, and 3.5 m. to Sanford.

Characteristics of the St. Johns River are low gradient, extensive tidal influence, and varying salinity and temperature. The river drops only about 6 m. in the 460 km. from its source to the ocean and has a slow current. The usual head of tidal influence is Lake George, 185 km. upstream. Salinity readings 15 km. from the mouth of the river ranged from 2.5 to 33.4 p.p.t. (parts per thousand) during 1961-62. They varied with depth, direction of the tide, and season (salinity was lowest in late summer and highest in late spring). South of Jacksonville, 40 km. from the mouth, salinity is normally less than 1 p.p.t. Water temperature between the mouth and Jacksonville ranged from a winter low of 8.2° C. to a summer high of 34.1° C.

ADULT CRABS

SEX COMPOSITION

Most of the blue crabs of commercial size (larger than 120 mm.) caught during most of the year in the lower river were females, but males were always dominant in the upper river. Among crabs caught in the first 24 km. of the lower river, 60 to 90 percent were females in January to September and 10 to 25 percent in October to December. In the next 24 km. of river, extending to 8 km. south of Jacksonville, females made up 75 percent of the catch in December to February and 15 to 55 percent in March to November. From a point about 8 km. above Jacksonville to Palatka the percentage of females ranged during the year from 10 to 35 percent; and above Palatka, from 5 to 35 percent.

Except in the fall when large numbers of males occasionally were captured very close to the jetties, nearly all of the adult blue crabs caught in the ocean were females.

MATING AND SIZE AT SEXUAL MATURITY

Female blue crabs mate once, after the last in a series of molts, but males may mate during each of their last three growth stages (Truitt, 1939). Before mating, the male carries the female beneath him, often for more than 2 days, until she sheds her immature shell. Sperm from the male is then

SPAWNING

transferred to the spermathecae of the female where it remains viable a year or more and is used for repeated spawnings.

Mating blue crabs were commonly observed from 11 to 215 km. above the mouth of the river. Primary mating areas were the shallower near shore waters of the main river and tributary streams. Mating occurred sparingly in January and February, was common in March to July, decreased sharply in late summer, and was common again in October to December. Among 25 randomly collected mating pairs that I measured, the smallest male was 121 mm. and the smallest female was 71 mm.

Maturity of blue crabs is attained at varying widths. The proportion of male and female crabs that matured at a small size was larger in salt water (from the mouth of the river to Jacksonville) than in fresh water (south of Jacksonville, table 1). The smallest mature female measured in the St. Johns River was 99 mm. and the largest immature female was 177 mm. Mature females believed to be *Callinectes sapidus* have been captured in North Carolina as small as 52 mm. (Fischler, 1959), but to my knowledge no immature female as large as 177 mm. has been reported for any other area. Overlap in the size ranges of immature and mature females in the St. Johns River was considerably greater than reported by Tyler and Cargo (1963) for Chesapeake Bay; their smallest mature female was 118 mm. wide and the largest immature female was 135 mm.

TABLE 1.—Percentage of mature male and female blue crabs in samples of commercial catches from the lower St. Johns River (salt water) and from the upper river (fresh water), 1961–62

Carapace width	Males				Females			
	Lower river		Upper river		Lower river		Upper river	
	Number examined	Mature	Number examined	Mature	Number examined	Mature	Number examined	Mature
Mm.	Number	Percent	Number	Percent	Number	Percent	Number	Percent
120–24	16	44	28	0	64	31	182	2
125–29	22	50	51	8	56	52	150	6
130–34	23	52	55	14	93	83	155	15
135–39	23	70	54	18	121	90	121	27
140–44	32	66	76	33	199	96	121	46
145–49	43	84	103	42	258	98	90	66
150–54	42	88	105	50	371	99	110	80
155–59	44	95	132	66	425	100	131	90
160–64	65	88	127	72	473	100	148	96
165–69	49	98	95	76	422	100	139	99

Intervals between mating and spawning of blue crabs, or migrations preparatory to spawning, vary with season. Spawning usually takes place within 1 to 2 months after mating in spring and summer. If crabs mate during fall or winter, spawning is delayed until warmer temperatures the following spring. Most mature females of the upper river migrate downstream to near Jacksonville (about 30 to 55 km. above the mouth) for maturation of the ovaries. In spring and fall, almost all females make the migration soon after mating and during early development of the ovaries. In summer and winter, however, more mature females delay migration downstream, and 20 to 50 percent of those in the upper river have large ovaries with well-developed eggs.

Most blue crabs spawn in the lower 32 km. of the river. Relatively few females spawn near Jacksonville, and I observed no spawning south of there. The eggs, numbering between 1 and 2 million and known as a sponge, are deposited on the abdominal appendages and carried by the female until they hatch. They are initially yellow-orange, but as the larvae develop and absorb the yolk during the 2 weeks required for hatching, the eggs become brown and finally black.

Spawning occurs in the St. Johns River 8 or 9 months of the year; only the very coldest winter months are excluded. In 1962, sponge crabs first appeared in the lower 32 km. of the river in February, were most abundant from March to September (when 40 to 82 percent of the mature females collected were with sponge), and were present through October. In 1963, sponges did not appear until March, probably because of the colder water in February. Water temperature in 1962 increased from an average of 13.2° C. in January to 18.4° C. in February. In 1963, water temperature decreased from 12.9° C. in January to 11.4° C. in February; in March it rose to 20.4° C.

As the eggs develop, the females move from the river into the ocean where the eggs hatch. Almost all of the sponges of river females are yellow-orange, whereas most sponges on blue crabs in the ocean are dark brown or black. Sponge crabs were first common in the ocean in March or April but only within 1 km. of shore at the river mouth. As the spawning season progressed, egg-bearing females were found over a wider and wider ocean

area. In June they were common out to 2.5 km., and from July through September, when they were most abundant, large numbers were 5 to 6 km. offshore between Fernandina Beach and Ponte Vedra Beach. The number of females offshore dropped sharply in October, but 62 percent were in sponge compared with 4 percent in the lower 32 km. of river. From November to February, female crabs were least common in the sampling area off the mouth of the St. Johns. During this period only one sponge crab was taken (in January) but the well-developed ova of most of the females indicated that they would spawn in the spring.

Many if not all female blue crabs spawn twice—in the same season or over two seasons—and they often return to inland waters to develop their second sponge. Throughout the spawning season, some females reentered the lower 40 km. of the river from the ocean and developed another sponge. These repeat spawners could be distinguished by the appearance of their shells. Crabs which have not left the river have shiny, clean, bright-colored shells. Crabs which have spent time in the ocean have dull-colored shells with an encrustation of fouling organisms—especially the turtle barnacle, *Chelonibia patula*. Blue crabs which had previously had sponges also could be distinguished by the ragged appearance of their abdominal appendages and the presence of egg-shell remnants.

TAGGING AND RECOVERY

The few tagging studies that have been made to determine movements of adult blue crabs have been confined largely to bays and to lower parts of estuaries. Fiedler (1930) found that tagged females released in the northern part of Chesapeake Bay migrated to the southern portion and tended to remain there. The direction of movement for males was random. Cronin (1954) detected no clear pattern for movements of crabs in Delaware Bay. Some males and females moved up Delaware Bay after wintering near the mouth; none of the tagged crabs was returned from other coastal regions. Cargo (1958), who tagged only females in Chincoteague Bay, Va., found they moved southward to the lower bay even if released in areas where high-salinity water was to the north. Only two crabs were captured outside Chincoteague Bay

—one at Oyster, Va., the other in Delaware Bay. Fischler and Walburg (1962) released 4,353 tagged blue crabs in three estuaries and two offshore locations in South Carolina. Both male and female crabs moved considerably between the lower estuaries and adjoining coastal waters. Only seven males and six females were recaptured in estuaries other than those in which the crabs were released. Crabs that entered estuaries were almost always from the adjacent ocean tagging site. All but two crabs were recaptured within 80 km. of the release area. The authors concluded that, in South Carolina at least, adult blue crabs do not migrate between estuaries but limit their movements to the estuary or adjacent marine area.

Of the 11,522 blue crabs tagged in the St. Johns River and in the ocean off its mouth, 4,059 (35 percent) were recovered. Ninety-seven percent of the recoveries were by commercial gear, which was fished every month of the year; 3 percent of the recoveries were by sport fishermen.

Return of tags from 2,839 males and 830 females recaptured after release in the river indicated some movement of both sexes throughout the year. Migrations within the river were principally downstream (table 2). Among crabs tagged from Jacksonville to Lake George and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured north or downstream from the point of release. Some males moved randomly between New Berlin and Picolata, but nearly all of those tagged south of Picolata were recaptured downstream. Females tagged at all sites during spring and summer usually migrated into the ocean within 1 month, but those tagged in late fall and early winter entered the ocean after 3 or more months. Only three females were recaptured more than 25 km. upriver from any tagging site. Many females from the upper river congregated near Jacksonville in late fall. They moved downstream to New Berlin as early as January but in greater numbers during March. Early in the spawning season (February–May) females were slower to spawn and lingered longer at New Berlin before entering the ocean than those of later months (May–September).

Two hundred thirty-five blue crabs (52 males and 183 females) tagged in the St. Johns River were recovered from other waters (fig. 3). Males entered the Intracoastal Waterway north of the

TABLE 2.—Number of tagged adult male blue crabs recovered after release at different localities in the St. Johns River

Locality of release ¹	Crabs tagged	Area of recovery (kilometers upstream from mouth of river) ²									Total recoveries
		215	195	170	135	95	70	40	15	0	
Km.	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Percent
195	1,287	5	481	74	19	36	7	1	2	2	49
170	790	1	18	274	53	58	6	2	3	0	53
135	717	0	0	2	151	109	12	5	6	1	40
95	1,474	0	0	1	2	575	41	43	16	6	46
70	738	0	0	0	0	35	219	32	11	3	41
40	599	0	0	0	0	1	5	203	22	10	40
15	778	0	0	0	0	2	2	32	220	30	37

¹ Kilometers upstream from mouth of St. Johns River.

² Approximate areas of recovery corresponding to kilometers upstream are:

215 km.—Astor; 195—Lake George; 170—Welaka; 135—Palatka; 95—Picolata; 70—Switzerland; 40—Jacksonville; 15—New Berlin; and 0—outside river.

St. Johns River and the Nassau River during all seasons of the year and migrated to the waterway south of the St. Johns River, to the Ft. George River, and to the ocean (from Fernandina Beach to Cocoa Beach) primarily during fall and early winter. Females migrated into the ocean from April through October. Most returns were from the vicinity of the mouth of the river, but others

ranged from Jekyll Island, Ga., to New Smyrna Beach, Fla. Sixty-six females recaptured in inland waters north of the St. Johns River were taken in the Intracoastal Waterway, the Ft. George, Nassau, St. Marys, and Crooked Rivers, and Kings Bay. Eight returns were from the waterway south of the St. Johns. Two of these crabs, which were tagged during late fall 1962, were recaptured dur-

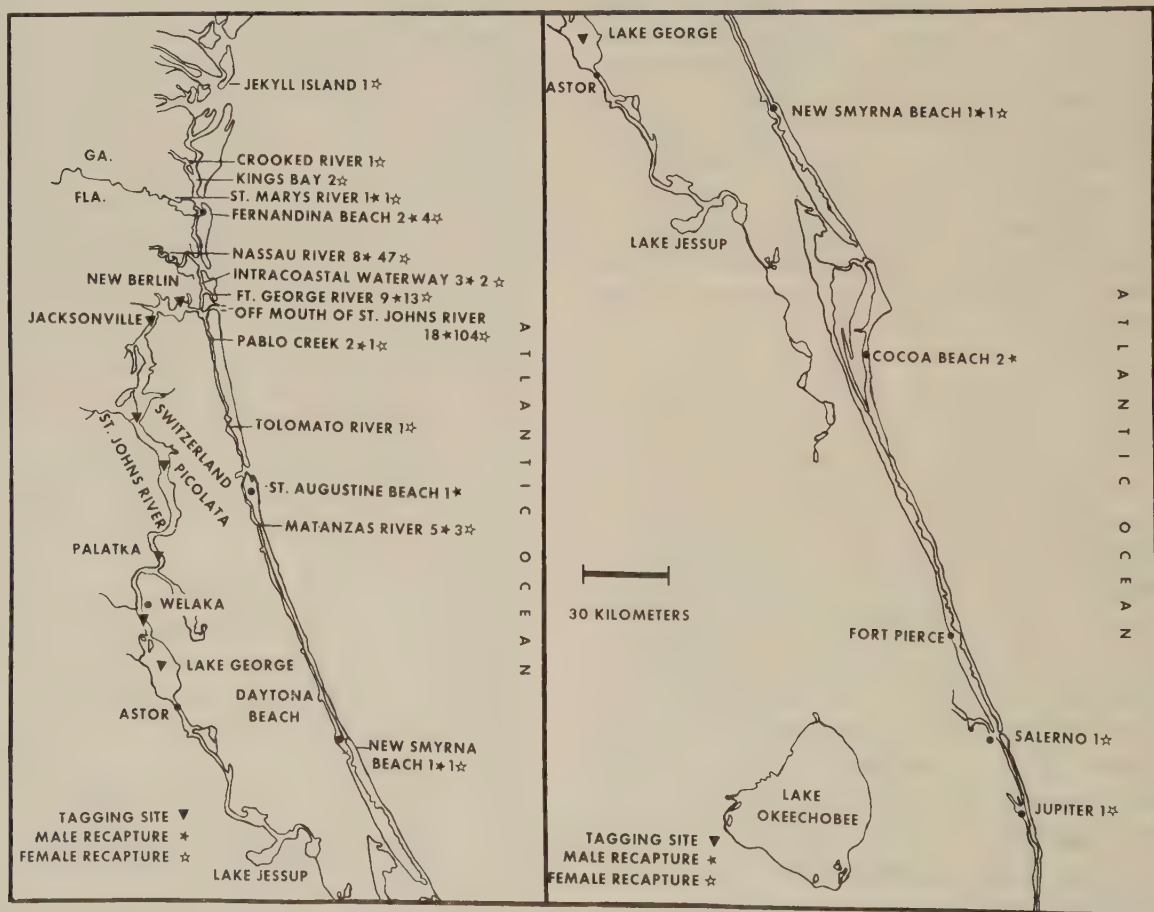


FIGURE 3.—Localities of recapture of blue crabs tagged in the St. Johns River that were recovered outside the river.

ing the succeeding winter near Salerno and Jupiter, about 460 and 540 km. from the point of release. The female recovered at Salerno traveled an average of at least 7.9 km. per day.

Some sponge female blue crabs migrated from New Berlin directly into the Intracoastal Waterway (north) and apparently entered the ocean by way of other rivers. Ten sponge females tagged at New Berlin (from April to September) were recaptured in the waterway and the Ft. George and Nassau Rivers within 3 to 14 days and before hatching in the ocean and return to inland waters were possible.

The migration of female blue crabs toward spawning grounds in high-salinity waters resembles that in other areas. The similar migration of at least some males, often parallel to females in time and distance, is unlike that reported elsewhere. In Chesapeake Bay, Van Engel (1958) reported that when females migrated downstream to the lower bay, adult males remained in brackish waters and many moved farther upstream.

Of the 381 tags recovered from female blue crabs tagged in the ocean off the mouth of the St. Johns River, 107 were from inland waters (fig. 4). Of these, 59 were recovered in the St. Johns River, 38 in the Nassau River, and the remainder in Cumberland Sound, Intracoastal Waterway, Crooked River, St. Marys River, and Ft. George River. Sixteen of the crabs that had been tagged off the mouth between May and January were recaptured in the St. Johns River during January, February, and March. These returns indicated, as did the composition of the commercial catches, that some crabs which spawned the previous season and others which matured and left the river in winter reentered the river before and during the earliest part of the spawning season. After their eggs hatched, females continued to enter the St. Johns and Nassau Rivers during summer and fall. Nearly all of the returns in the St. Johns River were between New Berlin and Jacksonville; a tag from Picolata was the only return upstream from Jacksonville. Returns from the Nassau River were mostly more than 11 km. from the mouth and extended upstream as far as 32 km.

Some female blue crabs reenter rivers very soon after their eggs hatch. From May through September, the majority of the returns in the St. Johns and Nassau Rivers of females tagged in the ocean

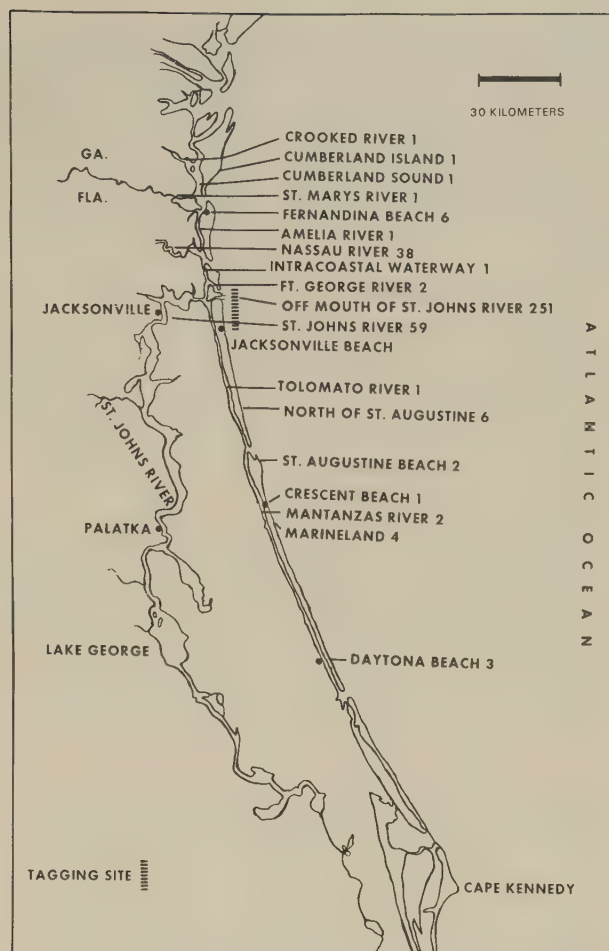


FIGURE 4.—Recovery locations of female blue crabs tagged in the ocean off the mouth of the St. Johns River.

(almost all in sponge or recently in sponge) came within 30 days, and most came within 15 days. Fifty-four of the sponge females tagged at New Berlin were recovered in the St. Johns and Nassau Rivers after more than 15 days, and, therefore, after hatching of the eggs. Of these, 40 were recovered in the rivers as soon as 16 to 45 days after release.

Eight of nine returns of male blue crabs tagged in the ocean off the mouth of the river were recaptured in that vicinity within 2 months. One male tagged in August was recovered in the Ft. George River in November.

LONGEVITY

In the St. Johns River, relatively few blue crabs survive more than 1 year after reaching maturity. We recovered only 13 tagged crabs more than 12

months after release. Three females were recaptured during the third spawning season, 20 to 24 months after they were tagged; and two males were recaptured after 33 and 36 months. If these periods are added to the approximately 12 months required to attain adult size, the maximum age of St. Johns crabs is estimated at little more than 4 years.

LARVAL STAGES

Newly hatched blue crabs pass through two larval forms, zoea and megalops. Rearing of larvae in the laboratory has shown that crabs have seven zoeal stages over a period of 31 to 49 days and a subsequent megalops stage of 6 to 20 days (Costlow and Bookhout, 1959).

Callinectes zoeae were found from April through October in samples taken between buoys 11 and 38, 3 to 11 km. above the mouth of the river. Peak abundance occurred earlier in 1962 than in 1961 (table 3). The number of zoeae per cubic meter of water ranged from 0 to 460.9. More *Callinectes*

zoeae were collected near the surface than at the bottom regardless of tidal direction. No evidence appeared of retention of *Callinectes* zoeae within the estuary, as more were obtained during outgoing tides than during incoming tides.

Most of the larval *Callinectes* captured were first-stage zoeae, but some second-stage zoeae and some megalops also were caught. The proportion of second-stage to first-stage zoeae was 1 to 323. The second-stage form occurred in one surface sample in May (1.5 per 1 m.³) and in four surface and four bottom samples in August (0.6–2.6 per 1 m.³). The proportion of megalops to zoeae was 1 to 164. Megalops were found in three July samples (0.5–1.1 per 1 m.³), two August samples (1.1–18.6 per 1 m.³), and two September samples (0.4 and 0.5 per 1 m.³). Ninety-six percent of the megalops were taken in bottom collections.

Zoeae of 22 kinds of crabs and megalops of 5 genera were collected between buoys 11 and 38. In 1961, *Callinectes* zoeae ranked third in abundance after *Uca* and *Sesarma* (table 4), and in 1962 *Callinectes* ranked second to *Uca* (table 5). Megalops of four other genera were collected from May through October. Sixteen samples contained *Uca*

TABLE 3.—Number of *Callinectes* zoeae collected per cubic meter of water in the St. Johns River between buoys 11 and 38 (3–11 km. above mouth of river)

Month and depth (meters)	1961			1962		
	Samples	Zoeae per 1 m. ³		Samples	Zoeae per 1 m. ³	
		Average	Range		Average	Range
	Number	Number	Number	Number	Number	Number
January:						
0.3				8	0	0
10.0				8	0	0
February:						
0.3				7	0	0
10.0				7	0	0
March:						
0.3				8	0	0
10.0				8	0	0
April:						
0.3				4	5.4	2.3–8.2
10.0				4	1.5	0–4.2
May:						
0.3	12	0.3	0–3.7	8	51.4	0–157.3
10.0	12	.7	0–7.6	8	18.2	1.1–52.4
June:						
0.3	11	6.2	0–24.0	16	53.8	0–460.9
10.0	11	2.0	0–8.3	16	24.2	0–129.0
July:						
0.3				8	6.2	0–23.7
10.0				8	6.9	0.5–22.3
August:						
0.3	8	119.5	16.9–358.0	23	4.0	0–25.2
10.0	8	82.8	12.1–221.8	23	1.7	0–9.0
September:						
0.3	8	.2	0–1.3	15	.9	0–4.1
10.0	8	.4	0–.9	15	.3	0–2.0
October:						
0.3	16	.1	0–1.4	14	.1	0–.8
10.0	16	.1	0–1.2	14	0	0
November:						
0.3	8	0	0	14	0	0
10.0	8	0	0	14	0	0
December:						
0.3	8	0	0			
10.0	8	0	0			

TABLE 4.—Estimated average number of crab zoeae per cubic meter of water, between buoys 11 and 38 (3–11 km. above mouth of St. Johns River) in May, June, and August–December, 1961

[Number of samples each month in parentheses]								
Species	May (24)	June (22)	Aug. (16)	Sept. (16)	Oct. (32)	Nov. (16)	Dec. (16)	Total (142)
	Number	Number	Number	Number	Number	Number	Number	Number
<i>Callinectes</i> sp.	0.5	4.1	101.2	0.3	0.1	0.0	0.0	106.2
<i>Emerita</i> sp.	1.0	.1	.0	.2	.0	.0	.0	.3
<i>Eurypanopeus</i> sp.	3.2	1.7	28.2	3.5	.9	.0	.0	37.5
<i>Hepatus</i> sp.	.0	.0	.8	2.4	.0	.0	.0	3.2
<i>Leucosiidae</i>	.0	.0	.2	1.0	.0	.0	.0	1.2
<i>Menippe</i> sp.	1.0	.6	1.5	3.1	.0	.0	.0	5.2
<i>Neopanope</i> sp.	.6	.0	2.5	.9	.1	.0	.0	4.1
<i>Pachygrapsus</i> sp.	.0	.0	.0	.0	1.0	.1	.0	.1
<i>Panopeus</i> sp.	.7	1.4	51.8	19.9	.1	.0	1.0	73.9
<i>Pilumnus</i> sp.	.0	.0	.0	.1	.0	.0	.0	.1
<i>Pinnixa</i> sp.	.4	.3	.7	10.2	.5	.2	.3	12.6
<i>Pinnotheres maculatus</i>	.0	.4	.8	.7	1.0	.1	.0	2.0
<i>Pinnotheres ostreum</i>	1.0	1.0	2.1	.2	.1	.0	.0	2.4
<i>Polonyx</i> sp.	.2	.0	.2	2.5	1.0	.0	.0	2.9
<i>Portunus gibbesii</i>	.0	.1	1.0	.8	.0	.0	.0	1.9
<i>Portunus sayi</i>	.2	.0	.0	.0	.0	.0	.0	.2
<i>Rithropanopeus</i> sp.	.8	.0	.1	.1	1.0	.0	.0	1.0
<i>Sesarma</i> sp.	2.5	6.3	104.4	6.6	.2	.0	.0	120.0
<i>Uca</i> sp.	4.4	29.3	742.5	18.5	.4	.0	.0	795.1
Unknown A.	.0	.0	1.0	.1	1.0	.0	.0	.1
Unknown D.	.0	.0	.0	.0	.0	.1	.0	.1

¹ Less than 0.06.

(0.6–59.6 per 1 m.³), 12 contained *Sesarma* (0.6–19.8 per 1 m.³), 10 contained *Neopanope* (0.5–9.7 per 1 m.³), and 9 contained *Panopeus* (0.5–2.3 per 1 m.³). Megalops of *Uca* and *Sesarma* were more abundant than *Callinectes*. As for *Callinectes*, 96 percent of the megalops of the other genera were from bottom collections.

Plankton collections were made also at buoy 63, 40 km. from the mouth of the river, during May and October 1961 and August 1961 and 1962 (table 6). *Callinectes* zoeae occurred in three May samples (1.2–4.7 per 1 m.³) and 10 August samples (0.9–6.1 per 1 m.³); 10 of these 13 samples were taken near the bottom. One bottom sample in May contained second-stage zoeae (2.4 per 1 m.³), and two bottom collections in August had megalops (both 1.2 per 1 m.³). *Rithropanopeus*, *Sesarma*, and *Uca* were the most abundant genera in the collections. Megalops collected in May were, in decreasing order of abundance, *Sesarma*, *Uca*, *Rithropanopeus*, and *Panopeus*. August samples contained megalops of only *Uca* and *Callinectes*.

Most of the larval *Callinectes* collected in the St. Johns River occurred at salinities and temperatures favorable to larvae reared in the laboratory. Laboratory-reared larvae of *C. sapidus* had a uniform rate of growth in salinities between 20.1 and 31.1 p.p.t. at 25° C. (Costlow and Bookhout, 1959). Even though almost all *Callinectes* larvae captured near the mouth of the St. Johns River (buoys 11–38) both at the surface and near the bottom were in favorable salinities, some of those captured up-

river (buoy 63) were in salinities which probably would be too low to sustain them over extended periods. Salinity near the mouth (surface and bottom) was between 25 and 35 p.p.t. from April to July and between 12 and 36 p.p.t. from August to October. Bottom salinity was nearly always greater than that at the surface, particularly during ebb tide. At buoy 63, larval *Callinectes* were captured in salinities from 9 to 27 p.p.t. Water temperature (April to October) in the lower 40 km. of river ranged from lows of 20° C. in April and October to a high of 31° C. in August. Temperature at the surface and bottom usually differed less than 1° C.

Plankton was collected between buoys 2 and 3 in south Jacksonville (48 km. above mouth of river) during August and October 1961. No *Callinectes* larvae were obtained. Zoeae and megalops of *Rithropanopeus* were predominant and present in almost all of the collections (zoeae: 0.7–61.7 per 1 m.³). Zoeae of *Uca* and *Sesarma*, many of them dead, were the only other larvae collected. Surface salinities in these months ranged from 0 to 10 p.p.t. and bottom salinities from 5 to 11 p.p.t.

Plankton collections made in the South Atlantic by the *Theodore N. Gill* in 1953–54 have been analyzed for the occurrence of *Callinectes* larvae (Nichols and Keney, 1963). Six stations were sampled off the mouth of the St. Johns River—one at the mouth, and five others, 32 km. apart, extending due east. Stages of zoeae found at the inshore station were the same as in the river—primarily

TABLE 5.—Estimated average number of crab zoeae per cubic meter of water, between buoys 11 and 38 (3–11 km. above mouth of St. Johns River) in January–November, 1962

[Number of samples each month in parentheses]

Species	Jan. (16)	Feb. (14)	Mar. (16)	Apr. (8)	May (16)	June (32)	July (16)	Aug. (46)	Sept. (30)	Oct. (28)	Nov. (28)	Total (250)	Rank in abundance
<i>Callinectes</i> sp.	0.0	0.0	0.0	3.4	34.8	39.0	6.5	2.8	0.6	10.0	0.0	87.1	2
<i>Dissodactylus</i> sp.	.0	.0	.0	.0	.2	.0	.0	.0	.0	.0	.0	.2	17
<i>Eurypanopeus</i> sp.	.0	.0	.2	1.0	11.1	5.4	.7	.9	1.6	.6	.0	21.5	5
<i>Hepatus</i> sp.	.0	.0	.0	.0	4.9	.3	1.0	.1	.4	.1	.0	5.8	9
<i>Leucostidae</i>	.0	.0	.0	.0	1.4	.1	1.0	.2	.1	.0	.0	1.8	12
<i>Mentippe</i> sp.	.0	.0	.0	.0	.1	.1	.4	.5	1.3	.2	.0	2.6	11
<i>Neopanope</i> sp.	.0	.0	1.0	2.4	4.8	1.2	.2	.3	.3	.1	1.0	9.3	6
<i>Pachygrapsus</i> sp.	.0	.0	.0	.0	.0	.0	.0	.0	1.0	.0	1.0	1.0	19
<i>Panopeus</i> sp.	.0	.0	.0	3.9	26.3	5.2	.9	1.2	.2	.1	.0	37.8	4
<i>Pilumnus</i> sp.	.0	.0	.0	.0	1.0	.0	.0	1.0	1.0	1.0	.0	1.0	19
<i>Pinnixa</i> sp.	.3	.2	1.0	.4	3.6	1.0	.3	.3	.7	.4	.3	7.5	7
<i>Pinnotheres maculatus</i>	.0	.0	.0	.0	.1	.8	.0	.2	.2	.1	.1	1.5	14
<i>Pinnotheres ostreum</i>	.0	.0	.0	2.3	2.4	1.3	.2	1.0	1.0	.1	1.0	6.3	8
<i>Polyonyx</i> sp.	.4	.0	.2	.4	.3	.1	1.0	1.0	.2	.1	1.0	1.7	13
<i>Portunus gibbesii</i>	.0	.0	.0	.3	.5	.0	.0	1.0	.0	.0	.0	.8	15
<i>Portunus sayi</i>	.0	.0	.1	.0	2.1	.6	1.0	.0	.0	.0	.0	2.8	10
<i>Rithropanopeus</i> sp.	.0	.0	.0	.1	1.0	.2	.0	1.0	.2	1.0	1.0	1.5	16
<i>Sesarma</i> sp.	.0	.0	.0	8.6	33.6	3.4	3.7	6.6	4.3	1.1	.0	61.3	3
<i>Uca</i> sp.	.0	.0	.0	63.5	137.6	17.2	7.0	5.5	4.2	2.5	.0	237.5	1
Unknown A.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.1	.0	.1	18
Unknown D.	.0	.0	.0	.0	.0	.0	.0	.0	.0	1.0	.0	1.0	19

¹ Less than 0.06.

TABLE 6.—Estimated average number of crab zoeae per cubic meter of water at buoy 63 (40 km. above mouth of St. Johns River) for certain months, 1961–62

(Number of samples each month in parentheses)

Species	May (16)	Aug. (38)	Oct. (16)	Range
	Number	Number	Number	Number
<i>Callinectes</i> sp.....	0.6	0.5	0.0	0– 6.1
<i>Eurypanopeus</i> sp.....	5.9	.2	.2	0– 21.5
<i>Menippe</i> sp.....	.0	1.0	.0	0– .7
<i>Neopanope</i> sp.....	1.9	.1	.0	0– 7.2
<i>Panopeus</i> sp.....	.4	.2	.0	0– 2.2
<i>Pinnixa</i> sp.....	.2	1.0	.1	0– 1.6
<i>Pinnotheres maculatus</i>	.2	.0	.0	0– 1.9
<i>Pinnotheres ostreum</i>	.1	1.0	.0	0– 2.1
<i>Portunus gibbesii</i>	.1	.0	.0	0– 1.1
<i>Portunus sayi</i>	.0	1.0	.0	0– .9
<i>Rithropanopeus</i> sp.....	25.2	22.4	.2	0–184.7
<i>Sesarma</i> sp.....	28.8	2.6	.0	0–132.6
<i>Uca</i> sp.....	112.3	6.5	.0	0–294.0

¹ Less than 0.06.

first but some second stage. All stages occurred at 32, 64, and 96 km. offshore. A few zoeae were obtained about 160 km. from shore. The relatively few megalops collected were at 64 and 128 km. offshore. *Callinectes* megalops were collected directly off the jetties in July, however, during limited sampling offshore in our study.

In brief, sampling for larval crabs in the St. Johns indicated that *Callinectes* was one of the most abundant forms in the region near the mouth. First- and second-stage zoeae entered and left the lower 40 km. of river from April to October. They were transported by surface and bottom currents; megalops usually were confined to the bottom. Early development occurs in the ocean within a few kilometers of shore, and growth after the second zoeal stage takes place farther offshore. Some larvae return to inshore waters as megalops.

JUVENILE CRABS

Although juvenile blue crabs were found in many localities from the mouth of the river to Astor, they usually occurred in small numbers or in larger numbers for short periods of time. Preferred habitats of those less than 40 mm. wide were in shallow water where the bottom consisted of either muck covered with dead plant material or firmer mud covered with dense growths of coontail (*Ceratophyllum*) and eelgrass (*Vallisneria*). Certain areas, where relatively large numbers of crabs congregated the year round, were selected for sampling at regular intervals in 1962 and 1963. These areas, and distances from the mouth of the St. Johns, were: Clapboard Creek (15 km.); Dunn

Creek (30 km.); Trout River (40 km.); buoy 24, Picolata (95 km.); and buoy 11, Palatka (135 km.).

Postlarval stages of crabs continue to molt periodically until full size is attained. The megalops molts directly into the first crab stage (2–3 mm. wide), which has the general appearance of the adult. Growth ceases after about 20 postlarval molts. Full size is attained in about 1 year; crabs shed every few days at the earliest stages and at intervals of 1 month or more at later preadult stages.

Early stages of blue crabs (2–9 mm. wide) entered the sampling areas in the lower 40 km. of river primarily as waves, beginning 5 or more months after spawning began and continuing to the end of the year. A few early crab stages appeared before this time, but only the occurrence of large numbers was considered a wave. The waves, except in early winter, were made up of crabs predominantly 6 to 9 mm. wide and beyond the initial crab stages. I collected few crabs 2 to 3 mm. wide during summer and fall. Escape of an appreciable number of first crab stages through the nets was unlikely as the catch in the stations of the lower river was always mixed with a great amount of mud and debris.

The area of metamorphosis of the megalops to the first crab stage has not been determined, but transformation probably takes place most frequently in the ocean. In the south Atlantic, most *Callinectes* megalops were found 64 or more kilometers offshore (Nichols and Keney, 1963). It is not surprising that we collected relatively few first and second crab stages in the river if transformation to the first crab stage also happens beyond 64 km. Some megalops may enter the first crab stage within the estuary, because megalops do appear in the river and directly off its mouth. Two megalops were collected along with early crab stages in Trout River.

The first waves of early crab stages in Dunn Creek and Trout River were in July 1962 and September 1963. With the early waves each year, abundance of individuals less than 20 mm. wide increase markedly (fig. 5). Like the initial spawning run, the first appreciable occurrence of young crabs was later in 1963 than in 1962.

First and second crab stages (2–4 mm. wide) predominated among early stages (2–9 mm. wide)

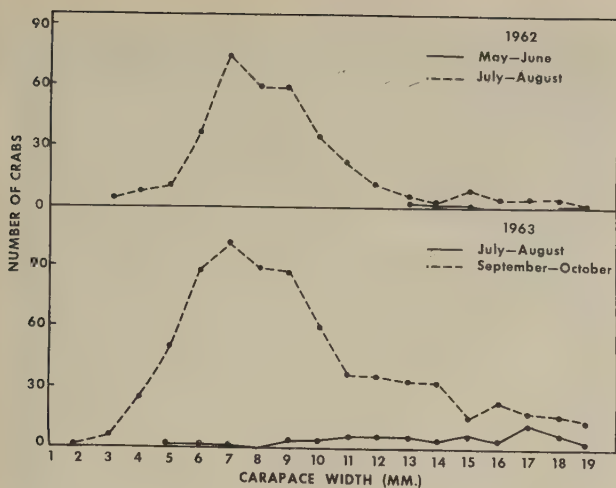


FIGURE 5.—Width distribution of blue crabs less than 20 mm. wide collected before and after the initial wave in Dunn Creek and Trout River.

in Dunn Creek and Trout River during December and January (fig. 6). These crabs were hatched in October and November, and subsequent winter temperatures probably inhibited postlarval growth. They shed throughout the winter but less frequently than in other seasons.

Waves of early blue crab stages also entered Clapboard Creek in 1962, but no appreciable influx was observed during 1963. Small numbers, including a few first crab stages, occurred among much larger numbers of *Callinectes similis* or *C. ornatus* from July to October 1963. No congregations of blue crabs developed, possibly because of competition for food and space from small juveniles of these other species, which were

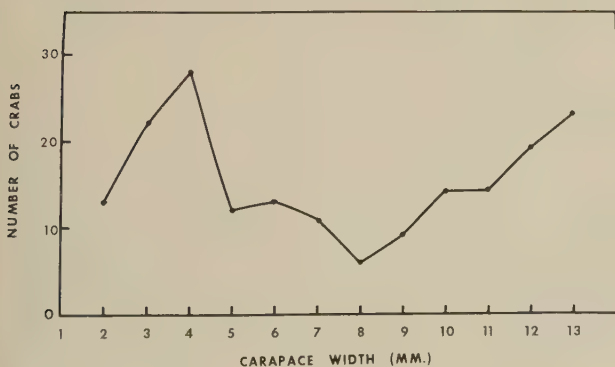


FIGURE 6.—Width distribution of blue crabs less than 14 mm. wide collected in Dunn Creek and Trout River during December 1962 and January 1963.

established in Clapboard Creek as early as May (Tagatz, 1967).

The influx of early crab stages was not confined to the lower river but extended 95 km. and more upstream. Early crab stages over 5 mm. wide first appeared at Picolata (buoy 24) during the same month as the initial waves in the lower river—July 1962 and September 1963. In 1962, most early crab stages were widely scattered in shallow areas adjacent to buoy 24; in 1963, waves and subsequent growth were clearly evident at this station (fig. 7). Crabs that made up the waves were larger than those entering lower river areas, and no crabs less than 6 mm. wide were caught. A few early crab stages 8 to 9 mm. wide were collected at Palatka (buoy 11).

In the St. Johns River, some juvenile blue crabs grew to maturity (or a harvestable size of at least 120 mm.) between the mouth and Jacksonville, but most females attained maturity between Jacksonville and Palatka; most males matured upstream of Palatka. Juvenile males were less abundant than juvenile females in the lower river, and the percentage of males increased with distance upstream (table 7). I found the largest concentrations of juvenile crabs 20 to 119 mm. wide at Picolata (buoy 24). Because of variation in growth rate and a long spawning season, significant numbers of crabs were one or more molts away from harvestable size during all seasons (table 8). Juveniles 20 to 39 mm. wide were most common in spring and fall. They were more widely distributed in the shallows along shore than larger crabs which remained in the channel. Juveniles 20 to 119 mm. wide also concentrated at Palatka (buoy 11). Upstream of Palatka, juveniles were nearly

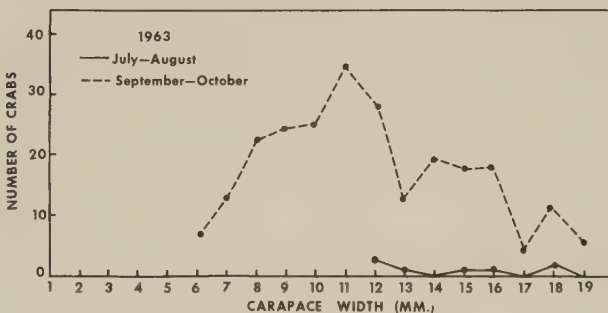


FIGURE 7.—Width distribution of blue crabs less than 20 mm. wide collected before and after the initial wave at Picolata (buoy 24).

TABLE 7.—Percentage of males among juvenile blue crabs collected at selected stations in the St. Johns River. Distance upstream in kilometers is shown in parentheses

Width	Trout River (40)		Buoy 24 Picolata (95)		Buoy 11 Palatka (135)	
	Crabs collected	Males	Crabs collected	Males	Crabs collected	Males
Mm.	Number	Percent	Number	Percent	Number	Percent
20-39	231	47	211	52	56	79
40-59	167	43	376	50	121	68
60-79	118	47	481	50	162	76
80-99	118	32	502	47	161	61
100-119	103	27	639	41	114	68
Total	737	41	2,209	47	614	69

all males and generally were larger than 100 mm. wide (relatively few males are available to the mature males that remain above Palatka). Juvenile blue crabs under 100 mm. and usually over 30 mm. occurred irregularly between Palatka and Welaka. Nearly all juveniles above Welaka were over 100 mm. wide; the smallest blue crab I caught was 25 mm.

In summary, juveniles, primarily beyond the initial crab stages, enter the St. Johns in waves during the latter part of the spawning season. The time of the first wave appeared to depend on the time of initial spawning. Many first and second crab stages entered in early winter. Individuals as small as 8 mm. wide moved at least 135 km. upstream. Juvenile blue crabs were widely distributed but concentrated the year around in certain localities. Those less than 40 mm. wide were most common in shallower waters; those more than 40 mm., in deeper areas. Females predominated in the lower river and males in the upper river.

FOOD OF BLUE CRABS

Blue crabs eat a great variety of foods. Fish, alive and dead, are eaten regularly (dead fish are used as bait in the commercial fishery). The diet of blue crabs includes many types of aquatic vegetation (Truitt, 1939), and they have been reported to eat oysters (Lunz, 1947) and other bivalves

(Carriker, 1951). Darnell (1958) found that blue crabs of Lake Pontchartrain, La., fed principally on mollusks (clams, mussels, and snails), crustaceans (mostly crabs but also barnacles and undetermined forms), and to a lesser degree on insects, hydroids, annelid worms, fish, algae, and vascular plants.

Little is known of the foods that sustain larval crabs. Most successful foods for growth of zoeae in the laboratory are yellow dinoflagellates (Sandoz and Rogers, 1944) and *Artemia* nauplii and *Arbacia* eggs (Costlow and Bookhout, 1959). The megalops is omnivorous and will eat pieces of fish, shellfish, and aquatic plants (Van Engel, 1958).

Of the 695 blue crab stomachs collected at four localities—Clapboard Creek (15 km. upstream from mouth of St. Johns River), Dunn Creek (30 km. upstream), Trout River (40 km. upstream), and buoy 24, Picolata (95 km. upstream)—668 contained food. Classes of food as percentage frequency of occurrence were:

Food item	Percent
Mollusks	32.4
Crustaceans	19.4
Organic debris	17.0
Fish	15.6
Plants	8.5
Annelids	5.0
Insects	1.4
Bryozoans	.6

Classes of food as percentage of the total volume of food per stomach were:

Food item	Percent
Mollusks	39.0
Organic debris	19.8
Fish	19.4
Crustaceans	15.0
Plants	3.9
Annelids	1.8
Insects	.9
Bryozoans	.1

TABLE 8.—Monthly size distribution of juvenile blue crabs collected at buoy 24, Picolata, St. Johns River, Fla., 1962

Width	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mm.	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
20-39	5	9	13	2	7	1	2	14	21	21	14	22
40-59	21	16	25	12	12	12	3	10	35	23	15	15
60-79	29	19	21	22	30	30	11	9	20	22	19	19
80-99	28	19	23	27	30	27	20	17	12	14	23	22
100-119	17	37	18	36	21	30	64	50	12	19	29	22
Total number of crabs	187	104	381	313	186	246	142	174	113	188	143	32

A large percentage of stomach contents consisted of organic material in advanced stages of digestion which could not be identified. Sand, mud, wood, charcoal, and similar debris (not recorded) were often taken by crabs incidentally in feeding. Sand, ranging from a single grain to several hundred grains, occurred in all gastric mills. A greater proportion of sand, relative to food content, was present in smaller crabs (less than 50 mm. wide) than in larger ones.

Generally all sizes of blue crabs ate the same types of foods (table 9) at all four stations sampled (table 10). Most of the mollusks eaten were mussels and clams. No mussels were found in crabs less than 21 mm. wide. Mussels eaten in the lower river stations (Clapboard Creek, Dunn Creek, and Trout River) were almost all *Modiolus demissus* but included a few *Musculus niger*. The only species present and eaten at Picolata was *Mytilopsis leucopheata*. Mussels were strongly predominant in crabs from Picolata where clams played a relatively minor role in the diet. Small numbers of *M. leucopheata* were present in Trout River, but none appeared in stomach samples. Mussels selected were less than an estimated 15 mm. long, and usually the shell in the stomach was fragmented. Very small mussels, 1.5 to 5.0 mm., were preferred; the gastric mill of adults often contained 25 to 50. Of the clams, Sphaerriidae, *Rangia cuneata*, and *Mulinia lateralis* were consumed, and probably other clams common to the lower river—*Tellina alternata*, *T. syharitica*,

Tagelus gibbus, and *Macra fragilis*. Crabs less than 21 mm. wide selected clams less than 2 mm., and even adults usually took clams under 10 mm. The stomachs of small crabs most often contained 5 to 10 clams, whereas those of larger crabs usually had 20 to 35 individuals. A few of the mollusks eaten were oyster spat, *Crassostrea virginica*, and snails, *Nassarius obsoletus* and possibly *Nassarius vibex* and *Neritina reclinata*.

Amphipods and crabs were the dominant Crustacea eaten. *Gammarus fasciatus* was taken at all stations, and *Corophium* sp. was a particularly important food of all sizes of blue crabs at Picolata. *Carinogammarus mucronatus* and *Talorchestia longicornis*, present in the lower river, probably were among other amphipods eaten. Crabs less than 31 mm. wide commonly had 10 to 15 amphipods in their stomachs. Of the crabs eaten, about one-half of those that could be identified were blue crabs and the remainder mud crabs—*Rithropanopeus harrisi* and probably *Panopeus herbstii* and *Eurypanopeus depressus*. No more than four individuals were in any food tract, and none appeared to have exceeded 20 mm. The mysid, *Neomysis americana* (listed as a shrimplike form), was taken fairly frequently, particularly in Clapboard Creek. Shrimplike forms as large as an estimated 30 mm. provided food but were too fragmented for positive identification. The most common shrimp at all stations were *Palaemonetes pugio* and *P. vulgaris*, and at Picolata, also *Macrobrachium ohione*. Ostracods

TABLE 9.—Food of the blue crab, by crab size, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach

[Number of stomachs with food in parentheses below designation of size group of crabs]

Food item	Width in mm.							
	5-10 (32)	11-20 (94)	21-30 (82)	31-40 (56)	41-50 (42)	51-100 (139)	101-200 (223)	Total (668)
Bryozoans		¹ 1 (0)			¹ 2 (0)	¹ 1 (0)	¹ 2 (0)	¹ 1 (0)
Mussels			5 (1)	9 (4)	10 (3)	34 (25)	46 (36)	24 (18)
Clams	9 (4)	31 (19)	49 (26)	38 (18)	33 (17)	34 (21)	32 (17)	34 (19)
Oysters						1 (1)	4 (2)	2 (1)
Snails				9 (4)	5 (3)	4 (1)	¹ 1 (0)	4 (1)
<i>Nereis pelagica</i>	¹ 6 (0)	7 (1)	13 (3)	18 (5)	24 (7)	10 (1)	¹ 2 (0)	10 (2)
Other annelids			21 (4)			¹ 1 (0)		¹ 0 (0)
Amphipods	6 (6)	3 (2)	18 (6)	12 (8)	17 (9)	27 (12)	10 (2)	14 (6)
Barnacles		¹ 1 (0)	¹ 1 (0)			¹ 1 (0)	¹ 2 (0)	¹ 1 (0)
Ostracods	9 (5)	¹ 2 (0)					¹ 1 (0)	¹ 1 (0)
Shrimplike forms			4 (2)	4 (2)	5 (5)	4 (1)	¹ 1 (0)	2 (1)
Crabs		¹ 1 (0)	10 (4)	12 (7)	12 (2)	19 (7)	13 (3)	12 (4)
Other crustaceans	28 (22)	23 (14)	8 (5)	11 (4)	7 (1)	5 (1)	1 (1)	8 (4)
Insects		6 (4)	5 (2)	7 (1)	¹ 2 (0)	¹ 1 (0)	¹ 1 (0)	3 (1)
Fish		16 (9)	39 (19)	27 (16)	38 (26)	32 (19)	38 (26)	31 (19)
Algae	12 (4)	16 (6)	11 (3)	14 (5)	14 (2)	4 (1)	¹ 3 (0)	8 (2)
Vascular plants		¹ 3 (0)	7 (1)	7 (1)	21 (6)	12 (1)	8 (2)	8 (2)
Organic debris	72 (59)	66 (43)	43 (24)	50 (24)	36 (17)	16 (8)	18 (10)	34 (20)

¹ Less than 0.6 percent.

TABLE 10.—Food of the blue crab, by crab size and by station, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach

[Stations and distance from mouth: 1-Clapboard Creek 15 km., 2-Dunn Creek 30 km., 3-Trout River 40 km., 4-Picolata 95 km. Number of stomachs with food in parentheses below designation of station]

Food item	Width in mm., station number, and number of stomachs with food											
	5-50				51-100				101-200			
	1 (55)	2 (120)	3 (100)	4 (31)	1 (31)	2 (15)	3 (37)	4 (56)	1 (67)	2 (34)	3 (46)	4 (76)
Bryozoans		¹ 1(0)	¹ 1(0)				¹ 3(0)			¹ 3(0)	¹ 2(0)	¹ 4(0)
Mussels			9(3)	13(5)	¹ 6(0)	7(3)	30(23)	61(44)	12(5)	15(11)	65(45)	79(68)
Clams	73(47)	27(13)	35(15)		58(31)	67(50)	43(28)	7(3)	43(31)	59(24)	35(20)	8(1)
Oysters					6(4)				12(7)	3(1)	¹ 2(0)	
Snails		¹ 1(0)	17(6)		3(1)		11(4)	¹ 2(0)	¹ 1(0)			¹ 1(0)
<i>Nereis pelagica</i>	5(2)	¹ 10(0)	31(9)		16(1)	¹ 7(0)	22(4)		¹ 3(0)	¹ 9(0)		
Other annelids							¹ 3(0)					
Amphipods	¹ 2(0)	2(1)	16(5)	48(30)	3(1)	¹ 13(7)		62(28)		¹ 3(0)		29(6)
Barnacles			¹ 2(0)			7(0)					2(1)	4(1)
Ostracods	5(3)		¹ 1(0)	3(2)								¹ 3(0)
Shrimplike forms	11(8)		¹ 1(0)		6(2)	7(1)	8(1)		¹ 3(0)		2(1)	16(3)
Crabs	¹ 2(0)	4(2)	12(5)	10(4)	10(5)	20(8)	32(14)	14(3)	12(2)	15(3)	11(3)	¹ 3(0)
Other crustaceans	16(8)	12(7)	15(8)	29(22)	¹ 3(0)		8(1)	5(2)				17(8)
Insects		9(4)	2(1)	6(1)			¹ 3(0)	¹ 2(0)		¹ 3(0)		¹ 1(0)
Fish	27(15)	28(16)	27(12)	10(10)	48(37)	40(25)	32(15)	20(11)	52(42)	62(39)	35(26)	17(8)
Algae	9(1)	9(5)	19(5)	22(4)	10(1)		3(2)	¹ 4(0)	¹ 3(0)	¹ 3(0)		5(1)
Vascular plants	5(2)	¹ 2(0)	13(2)	10(2)	¹ 10(0)	20(1)	16(2)	9(2)	4(2)	15(2)	¹ 2(0)	12(4)
Organic debris	38(13)	64(49)	51(28)	45(21)	19(16)	7(5)	16(6)	16(6)	18(11)	24(19)	9(3)	21(9)

¹ Less than 0.6 percent.

were an important food of 5- to 10-mm. crabs. Barnacles were infrequent foods but as many as 50 small *Balanus eburneus* were eaten by a 124-mm. crab at Picolata. Many crustaceans were too decomposed or fragmented to classify—particularly microcrustacea in crabs less than 21 mm. Some of the larger fragments closely resembled isopods.

Fish was a major food, especially of larger crabs. Ingested fish could not be identified, but distinguishable parts indicated that small and large fish of many species were eaten. No fish was observed in crabs less than 11 mm. wide.

Algae and vascular plants were frequent in the stomachs of blue crabs. Algae with the exception of *Ulva* were not identified but most often occurred as many filaments. Crabs ate the leaves, stems, roots, and seeds of various species of higher plants (only *Ceratophyllum* and *Vallisneria* were identified). Occasionally 20 to 30 small uniform-sized pieces of *Vallisneria* leaves in a stomach appeared to have been eaten from the plant.

Among lesser food items, *Nereis pelagica* was regularly consumed by all sizes of crabs at the lower river stations. Other annelids were taken infrequently at Trout River and Picolata. Insects were eaten at all stations except Clapboard Creek. Each stomach always contained several individuals. Gastric mill contents included adults of Coleoptera, Diptera, Hemiptera, and Hymenop-

tera, and young of Diptera and Odonata. Bryozoa occurred only as occasional fragments.

Blue crabs often ate the same food items during each of the three seasons of sampling (table 11), and they usually consumed the most available foods. The largest numbers of mussels were eaten in spring and summer when young mussels (less than 5 mm.) were first abundant. We found clams of all sizes common in the lower river during all seasons. Because small clams were uncommon at Picolata the abundant mussel population probably was utilized to a greater degree. Oysters and snails (particularly *Nassarius obsoletus*) were common in the lower river but provided only limited amounts of food. Amphipods were most abundant at Picolata, where they were consumed most extensively. Young blue crabs and mud crabs were common in all months of sampling, but relatively few occurred in the food tracts in winter. Shrimplike forms were not eaten in proportion to the large number generally present at all stations. We collected many fish of all sizes the year around. The percentage eaten was smaller at Picolata than at the lower river stations, which served as nursery areas for a greater variety of abundant species. Consumption of fish was high during winter before recruitment of young mussels. Although aquatic plants grew most profusely at Picolata, they were not a preferred food.

TABLE 11.—*Food of the blue crab, by crab size and by season, in the St. Johns River as percentage frequency of occurrence and (in parentheses) as percentage of total volume per stomach*

[Number of stomachs with food in parentheses below designation of season]

Food item	Width in mm., season, and number of stomachs with food								
	5-50			51-100			101-200		
	Dec.-Feb. (61)	Mar.-May (160)	June-Aug. (85)	Dec.-Feb. (21)	Mar.-May (74)	June-Aug. (44)	Dec.-Feb. (25)	Mar.-May (143)	June-Aug. (55)
Bryozoans.....		¹ 1 (0)			¹ 1 (0)			¹ 2 (0)	¹ 4 (0)
Mussels.....		4 (2)	7 (2)	14 (9)	44 (35)	27 (15)	20 (14)	52 (42)	42 (29)
Clams.....	26 (13)	34 (20)	44 (20)	24 (15)	28 (20)	50 (26)	40 (31)	28 (13)	38 (22)
Oysters.....						4 (3)		6 (2)	4 (2)
Snails.....		2 (2)	16 (4)		¹ 3 (0)			¹ 1 (0)	¹ 2 (0)
<i>Nereis pelagica</i>		17 (4)	18 (4)		9 (1)	16 (2)		¹ 3 (0)	
Other annelids.....	¹ 6 (0)			¹ 5 (0)	¹ 1 (0)				
Amphipods.....	5 (3)	11 (5)	16 (7)	28 (14)	24 (11)	32 (13)	12 (1)	¹ 6 (0)	22 (6)
Barnacles.....		¹ 1 (0)	¹ 1 (0)			¹ 2 (0)			7 (2)
Ostracods.....	2 (1)	1 (1)	¹ 2 (0)					¹ 1 (0)	¹ 2 (0)
Shrimplike forms.....	6 (5)	1 (1)	¹ 2 (0)	10 (2)	¹ 3 (0)	¹ 4 (0)		¹ 1 (0)	¹ 2 (0)
Crabs.....	3 (2)	7 (4)	9 (2)		22 (8)	23 (8)		11 (2)	25 (7)
Other crustaceans.....	18 (14)	13 (6)	18 (12)	5 (1)	¹ 3 (0)	9 (3)		¹ 1 (0)	
Insects.....	¹ 2 (0)	6 (3)	6 (2)		¹ 1 (0)	¹ 2 (0)		¹ 1 (0)	¹ 2 (0)
Fish.....	30 (23)	20 (11)	33 (13)	57 (44)	24 (14)	32 (16)	48 (42)	41 (27)	25 (17)
Algae.....	23 (10)	17 (5)	¹ 1 (0)	24 (3)	1 (1)		24 (3)	¹ 1 (0)	
Vascular plants.....	5 (1)	8 (1)	7 (2)	¹ 5 (0)	14 (2)	14 (1)	¹ 8 (0)	9 (3)	5 (1)
Organic debris.....	38 (28)	56 (36)	60 (31)	14 (10)	15 (6)	18 (10)	12 (9)	17 (9)	24 (12)

¹ Less than 0.6 percent.

The year-round abundance of preferred food items undoubtedly is a major cause for the large concentrations of juvenile blue crabs near Picolata. Random sampling with trawl and dredge below Picolata (between buoys 18 and 22) in summer indicated relatively less plant cover and less food, particularly amphipods and mussels. Juvenile crabs that fed on mollusks in the lower river conceivably are attracted to an accustomed food, such as mussels, at Picolata. Crabs also benefit from an interesting food chain transition at buoy 24. Young mussels occur most commonly within large clam valves. When the mussels are chewed off, chironomid larvae build algal tunnels on which amphipods feed and provide a second feeding for crabs.

In brief, blue crabs 5 to 200 mm. wide fed principally on mollusks, fish, and crustaceans and to a lesser degree on plants, annelids, insects, and bryozoans. Crabs generally ate the same type of food regardless of crab size, area, and season. They usually consumed the most available foods.

SUMMARY

Studies on the biology of the blue crab in the St. Johns River were made to obtain information necessary to determine factors which affect the harvestable population.

Females made up the majority of adult crabs during most of the year in the lower St. Johns River, but males were dominant in the upper river.

Blue crabs commonly mated from March to July and from October to December. The proportion of males and females that matured at a small size was larger in salt water than in fresh water. Size at maturity varied widely as evidenced by a 177-mm. wide immature female and a 99-mm. mature female; some of this variation can be attributed to individual differences in growth rate.

Spawning occurred in the first 30 km. of river above the mouth, and the eggs hatched in the ocean within 6 km. of shore. Spawning began in February 1962 and in March 1963 and continued to October in both years. An appreciable number of ovigerous females from the St. Johns River apparently entered the ocean by way of the Intra-coastal Waterway and other rivers. Some females entered the river from the ocean before the spawning season. Many others returned to the St. Johns River or entered other rivers, often within 15 days after their eggs hatched, to spawn a second time in the same season.

Of crabs tagged 40 to 195 km. above the mouth and recovered at a distance from the tagging site, 89 percent of the males and 96 percent of the females were recaptured downstream from the point of release. In fall and early winter, females from the upper river congregated 30 to 55 km. above the mouth. During the same period aggregations of males appeared nearer the mouth and in the ocean directly off the mouth. Crabs of both sexes mi-

grated from the St. Johns River to the Intracoastal Waterway, to four other rivers, and to the ocean.

Females tagged in the ocean off the mouth of the river were recaptured in the St. Johns River and other inland waters; in addition widespread recoveries were made in the ocean.

Time between tagging and recoveries indicated that relatively few blue crabs live longer than 1 year after becoming adults. Maximum age is about 4 years.

Zoeae—primarily first stage but some second—and megalops of crabs of the genus *Callinectes* were collected in the river as far as 40 km. from the mouth. Zoeae were present in April to October. Of 22 kinds of crab zoeae collected near the mouth, *Callinectes* ranked third in abundance in 1961 and second in 1962.

Early crab stages (2–9 mm. wide) entered lower river areas primarily in waves which started 5 or more months after spawning began and continued to the end of the year. Most individuals in these waves were beyond the initial crab stages except during early winter. The time of the first waves was later in 1963 than in 1962, probably because of the later spawning season in 1963. Influx of early crab stages was not confined to the lower river but extended 95 km. and more upstream.

Juvenile crabs of many sizes were widely distributed but were concentrated the year around in certain localities. Those less than 40 mm. wide were most common in shallower waters. Juvenile females outnumbered juvenile males in the lower river, but the percentage of males increased with distance upstream.

Crabs 5 to 200 mm. wide fed principally on mollusks (primarily clams and mussels), fish, and crustaceans (mostly amphipods and crabs). Lesser amounts of plants, annelids (almost all *Nereis pelagica*), insects, and bryozoans were eaten. Usually the same types of foods were taken by all sizes of crabs and at all areas sampled. Crabs often ate the same foods during different seasons and generally consumed the most available foods.

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PASSAGE OF ADULT CHINOOK SALMON THROUGH BROWNLEE RESERVOIR, 1960-62

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ABSTRACT

Adult chinook salmon (*Oncorhynchus tshawytscha*) were tagged and released in Brownlee Reservoir and upstream in the Snake River to determine if adults could pass through the reservoir and reach spawning grounds. Experiments with Petersen disk tags were performed by the Idaho Fish and Game Department in 1960-61 and by the Department and the Bureau of Commercial Fisheries in 1962. In addition, the Bureau marked salmon with sonic tags in 1961-62 to trace orientation and movement. Information was also obtained on the use of tributary streams for spawning and success of spawning.

Fish marked with Petersen disk tags and released in the 92.5-km.-long reservoir reached their spawning area as successfully as those transported above the impound-

ment and released in the river. Fish released during periods of constantly high water temperature in 1961-62 suffered losses, which may have been caused by stress during tagging. Some salmon with sonic tags were initially disoriented when released in the reservoir; those released in the river above the impoundment quickly oriented to the flow and resumed migration upstream.

Subpopulations of spring- and fall-run chinook salmon continued to use ancestral spawning areas in streams tributary to the impoundment after it was formed in 1958. No differences were noted between percentages of totally spent fall-run fish on the spawning grounds in the years before and after Brownlee Reservoir was filled.

Knowledge of the effect of impoundments on upstream migration is needed to plan the passage of adult salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) at high dams. If mortality is high in the reservoir, or if delays or other factors associated with passage impair the ability of survivors to spawn, the fish may have to be transported around the impoundment. Transportation could prove difficult if spawners bound for several tributaries were intermingled below the dam. Subpopulations would then have to be separated before their release into respective tributaries—a difficult or impossible task. On the other hand, if anadromous fish can migrate up through the

impoundment and spawn successfully, they can be passed directly to the forebay of the dam to continue their natural migration upstream.

Neither Brownlee Dam nor Oxbow Dam, which is 19.3 km. downriver from Brownlee, has a fishway leading up to its impoundment. Migrating adults enter a collection facility at Oxbow Dam where they are trapped and transferred to a tank truck; they are then transported 23.3 km., to a point 4.0 km. above Brownlee Dam, and released into Brownlee Reservoir to resume their migration. Release of fish in the reservoir was discontinued after these studies were completed; all fish were transported to hatcheries for artificial propa-

gation. A small hatchery for fall chinook salmon (*O. tshawytscha*), 1 km. downstream from the trapping site, has been operated at Oxbow Dam from 1960 to the present by the Idaho Fish and Game Department.

Fishery agencies recognized that Brownlee Reservoir posed a number of problems. The impoundment is 92.5 km. long; it has almost no current except during periods of high river discharge and extreme drawdown; water temperatures are high and oxygen concentrations are low during summer and early fall when spawning migrations occur.

To learn if adults could pass successfully through Brownlee Reservoir and reach the spawning grounds, the Idaho Fish and Game Department tagged fall chinook salmon (with Petersen disk tags) in 1960-61. The Bureau of Commercial Fisheries, in cooperation with Idaho, continued the investigations in 1962. Petersen disk tags were used in all years; the Bureau also used sonic tags in 1961-62 to trace the orientation and movement of fish.

This report summarizes the results of the 1960-62 studies. It also contains information on (1) orientation and migratory behavior of sonic-tagged salmon, (2) observations of totally spent fish in the Snake River above Brownlee Reservoir, and (3) use of tributary spawning streams after completion of Brownlee Reservoir.

METHODS AND MATERIALS

The general plan was to capture adult chinook salmon in a trap at Oxbow Dam and transport them upstream for release either in Brownlee Reservoir or in the Snake River above the reservoir (fig. 1). Some of the fish released in the reservoir were either tagged or fin clipped; others were caught and released unmarked without additional handling. The relative numbers recovered on ancestral spawning grounds below Swan Falls provided data that enabled us to measure the ability of migrants to pass through Brownlee Reservoir. Sonic tags were applied to 59 fish in 1961-62 to obtain information on orientation and migratory behavior in and above the impoundment. A summary of data on tagging and release is shown in table 1.

CAPTURE AND HANDLING

Adult chinook salmon used in the experiments were taken at different stages of the spawning run in the different years. In 1960 and 1961 the fish were obtained after the peak of the run. Hauck (1961)¹, describing the work in 1960, mentioned "... that the selection of fish for tagging was not on a random basis; that some selection was made for better fish on the basis of appearance and physical vigor."

¹ Hauck, Forrest. 1961. Fall chinook salmon tagging studies, Snake River, 1960. Idaho Fish and Game Dept., 7 pp. [Processed.]

TABLE 1.—Summary of data on tagging and release during tests on passage of fall-run chinook salmon through Brownlee Reservoir, 1960-62

[Unmarked fish were released in the reservoir during normal transport to maintain run; all fish were taken from trap at Oxbow Dam (fig. 1)]

Year and kind of mark	Released in reservoir			Released in river		
	Date	Number	Anesthetized ¹	Date	Number	Anesthetized ¹
1960						
Petersen tag	Sept. 20-21	108	No	Sept. 23-30	267	No
Do	Oct. 4-7	253	No	-----	----	----
None	Aug. 4-Dec. 12	4,282	No	-----	----	----
1961						
Petersen tag	Sept. 18-Oct. 31	686	Yes	Sept. 18-Oct. 31	688	Yes
None	Aug. 9-Dec. 10	3,272	No	-----	----	----
Sonic tag	Sept. 20-Oct. 21	15	No	-----	----	----
1962						
Petersen tag	Aug. 27-Oct. 21	444	Yes	Aug. 27-Oct. 21	340	Yes
None	Aug. 20-Dec. 11	342	No	-----	----	----
Fin clip	Aug. 27-Oct. 21	365	Yes	-----	----	----
Sonic tag	-----	----	----	Sept. 24-Oct. 8	44	Yes

¹ Anesthetized for tagging, but not during transport to release site.

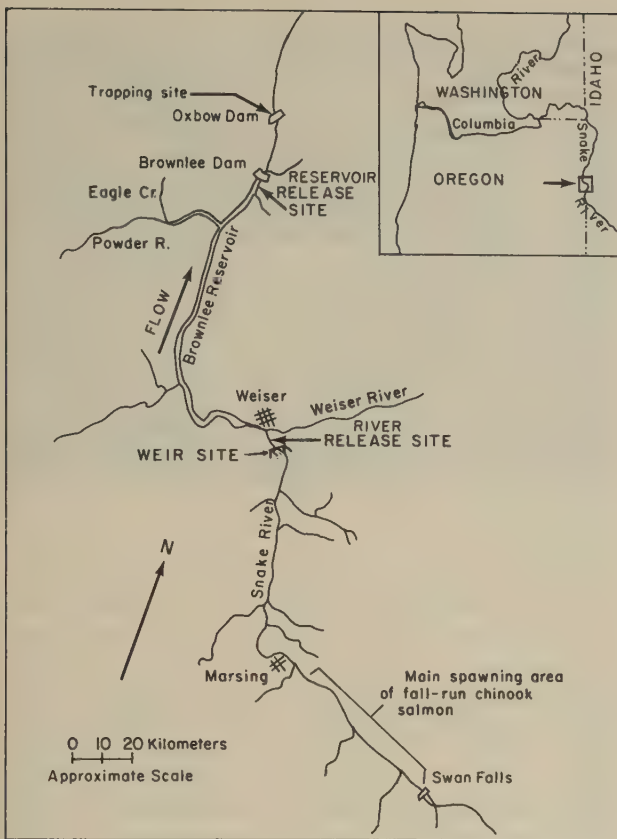


FIGURE 1.—Map showing trapping site below Oxbow Dam, release sites in and above Brownlee Reservoir, weir site, and main spawning area of fall-run chinook salmon in the Snake River, 1960–62.

In 1961, fish were collected in the trap until numbers were sufficient for tagging. The trapping time ranged from a few hours, soon after the peak of the run (when the tests started), to 1 day in the later stages of the run. In 1962, the trapping to obtain fish for tagging and release was scheduled by stage of migration. In the early and late stages (August 20 to September 23 and October 15–21) fish were collected for 24 hours before they were removed to the tagging area, and during the peak of migration (September 24 to October 14) fish were removed from the trap for tagging after about 30 had accumulated.

Fish were transported in a tank truck (3,785-liter capacity); water was recirculated and, except for a few hauls in 1960, oxygenated. Ice was used to control water temperatures

during the 3½-hour drive to the release site at the river, but not during the 1-hour drive to the release site at the reservoir.

All salmon were anesthetized (with tricaine methane sulfonate) for tagging in 1961–62, but not in 1960; none were anesthetized during transportation.

Prophylactic treatments, supervised by the Fish Commission of Oregon, were used in 1962 to attempt to minimize the transmission of disease among fish during tagging and close confinement in the tank trucks. Prophylactics included tincture of iodine, roccal, ethanol, and malachite green. Tagging equipment was sterilized in a 70 percent solution of ethanol; the tagging area on the fish was treated with iodine. Wounds, abrasions, and infected areas were treated by topical application of a 15 percent solution of malachite green. In addition, all fish were treated for 1 hour with 1 p.p.m. (parts per million) of malachite green while being transported to the release sites. At the end of a day's operation, fish tanks on the hauling trucks were sterilized with roccal.

Skin discoloration and formation of blisters early in the experiment indicated that the iodine treatment might be affecting the fish adversely. As a precautionary measure, a 15 percent solution of malachite green was used in lieu of the iodine after the third week of tagging. On one occasion the fish tank was inadequately rinsed and the remaining roccal killed a load of fish. Thereafter malachite green at a concentration of 2 p.p.m. was used instead of roccal for sterilization.

TAGGING AND RELEASE

Petersen disk tags, sonic tags, and adipose fin-clips were used to mark adult chinook salmon before they were released. Personnel of the Idaho Fish and Game Department applied all disk tags (fig. 2), which were numbered or multicolored for identifying individual fish. The Bureau of Commercial Fisheries attached all sonic tags; only fish over 61 cm. were tagged. The Bureau also excised the adipose fins.

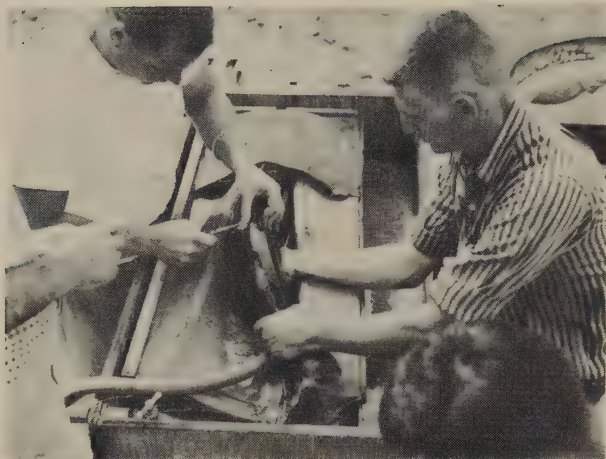


FIGURE 2.—Personnel of the Idaho Fish and Game Department attaching disk tag to chinook salmon. Fish is partially submerged in water supplied by hose in left foreground. Canvas cover over head of salmon helps quiet it during tagging.

Petersen Disk Tag

Tagging and release of disk-tagged fish differed in certain details during the 3 years of the study. In 1960, fish were tagged at the Oxbow trap and transported directly to release sites in the river or the reservoir. In 1961, untagged fish were transported to the release site and discharged into a holding pen; individual fish were then removed, anesthetized, tagged, and released at the site. In 1962, fish were taken from the Oxbow trap in groups of as many as 30, anesthetized en masse, tagged, put in a tank truck with fresh water to recover, hauled to the river or reservoir release site, and discharged into an open-ended holding pen. They swam over a submerged weir at the open end of the pen to resume migration. Individuals that did not leave the pen in 24 hours were eliminated from the experiment.

Releases of tagged and untagged fish in 1962 varied between migration periods. During the early and late stages of migration, fish were released daily for 6 successive days at a single site. For example, tagged fish were released in the Snake River on the first day of a week and in the reservoir on the next day. On the third day of the series, only untagged fish were released in the reservoir. This sequence was re-

peated over the next 3 days. No tagging was done on the seventh day, but fish captured in the trap at Oxbow Dam were transported and released in the reservoir by the Idaho Power Company as part of their usual fish-passage work. At the peak of migration (September 24 to October 14), tagged fish were released daily at both sites for 5 days a week. No more than 30 fish with Petersen tags were released at either site on any day. (In this same period, fin-clipped fish were released in the reservoir along with untagged fish that were excess to the tagging needs.) On the other 2 days of the week, only untagged fish were released in the reservoir.

Fin Clip

Fish marked by an adipose fin clip were released at the reservoir site only in 1962. These fish had been anesthetized and inspected during selection for spawn taking at the Oxbow hatchery but were not retained for that purpose. They were fin clipped to differentiate them from untagged fish that were released during the early stage of the 1962 experiment (September 10–16), but most were released during the peak stage of migration (September 24 to October 14).

Sonic Tag

Each sonic tag, used in 1961–62, was fastened by a metal clip or hog-ring which was crimped into the flesh behind the dorsal fin. The battery-powered tags emitted 132-kc. signals, detectable by receiving equipment within a range of about 1 km.; the operational life was about 5 days.

Salmon bearing sonic tags were released only in the reservoir in 1961 and only in the Snake River in 1962. In 1961, they were tagged at the reservoir release site and allowed to resume their migration from an open-ended holding pen. In 1962, the fish were tagged in groups of 6 to 14 at the Oxbow trap, coincident with the Petersen-disk tagging, and transported with the other tagged fish to an open-ended holding pen at the Snake River release site.

The sonic tags enabled us to obtain detailed



FIGURE 3.—Boat following chinook salmon with sonic tag in Brownlee Reservoir. Electronic tracking equipment provided precise data on day and night movements of tagged fish.

information on movements of individual fish in the reservoir by tracking them in a boat equipped with receiving equipment and plotting their positions on a chart at about 5-minute intervals (fig. 3). In the Snake River, the date and time of passage of fish with sonic tags past specific points was automatically recorded on time-event charts connected to fixed monitors² placed along the shoreline (fig. 4). Information on movement of individuals and groups of tagged fish between monitoring stations was obtained with portable hydrophones on a skiff propelled by an outboard motor.

RECOVERY

Marked and unmarked chinook salmon were recovered from the spawning area in periodic surveys from October to mid-January. The surveys were made monthly for the 1960 spawning run by the Idaho Fish and Game Department and weekly for the 1961 and 1962 runs, when the Bureau of Commercial Fisheries assisted the Department.

During the surveys, observers drifted downstream in a small boat or waded through shallow areas to search the entire known spawning area for carcasses. The dead salmon were ex-

² Johnson, James H. 1963. Development and use of sonic tracking as an aid to Pacific salmon conservation studies, 13 pp. [Processed.]

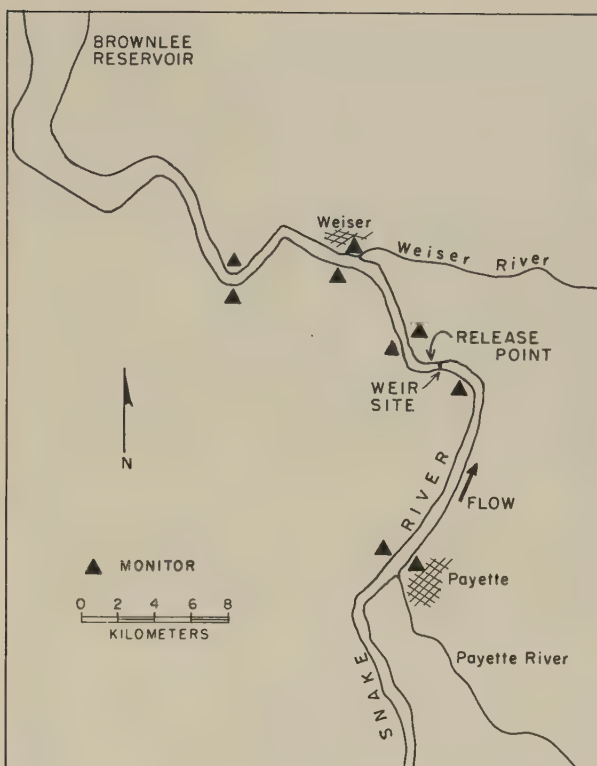


FIGURE 4.—Locations along Snake River between Brownlee Reservoir and the mouth of Payette River where fixed monitors recorded the passage of upstream-migrating chinook salmon carrying sonic tags.

amined for tags, fin clips, and spawning stages and then marked with spaghetti-type tags to identify them on future surveys. SCUBA diving was added in 1962 for investigation of deep pools where the spent fish might accumulate and remain unobserved. The greater recovery effort in 1962—plus experience gained in searching for fish in 1960–61—may have led to higher rates of recovery of untagged fish in 1962 (24.9 percent) than in 1960 (5.1 percent) or 1961 (14.3 percent). Water level and clarity appeared to be about the same for the 3 years.

PROPORTIONS OF FISH REACHING SPAWNING GROUNDS

In evaluating recoveries from both release sites, we considered the possible effect of differences in hauling time and post-release environment on the eventual passage of chinook salmon to the spawning grounds. Differences in haul-

ing time, however, did not appear to be an important factor in survival. Although fish transported to the Snake River were confined in a tank truck about 2½ hours longer than those transported to the reservoir, they appeared to be in excellent condition at release. Other investigators have also indicated that prolonged transportation is not detrimental to adult chinook salmon. Parker and Hanson (1944) successfully transported adult salmon for 2 hours, and Fish and Hanavan (1948) reported hauls of about 4 hours without adverse effects. Groves (personal communication³) transported adult chinook salmon for about 5 hours to a test area in 1961 and followed this at a later date by a 5-hour return haul to a hatchery. He reported no mortalities directly attributable to the prolonged transportation.

Differences in postrelease environment also had no apparent effect on survival in the present experiments. Differences between recoveries of tagged fish released in the reservoir and of those released in the river were not significant in any year (table 2).

TABLE 2.—Numbers of marked and unmarked fall-run chinook salmon released in Brownlee Reservoir and the Snake River and numbers recovered on the spawning grounds, 1960–62

Year and release site	Mark ¹	Fish released	Fish recovered on spawning grounds	
			Number	Percent
1960 ²				
Reservoir	Tag	361	23	6.4
	None	4,282	218	5.1
River	Tag	267	16	6.0
1961 ³				
Reservoir	Tag	686	70	10.2
	None	3,272	467	14.3
River	Tag	688	83	12.1
1962				
Reservoir	Tag	444	13	2.9
	Fin clip	365	31	8.5
	None	342	85	24.9
River	Tag	340	11	3.2

¹ Tag indicates Petersen disk; none of the 59 fish tagged with sonic tags were recovered.

² Hauck, Forrest. 1961. Fall chinook salmon tagging studies, Snake River, 1960. Idaho Fish and Game Department. 7 pp. [Processed.]

³ Graban, James R. 1964. Evaluation of fish facilities, Brownlee and Oxbow Dams, Snake River. Idaho Fish and Game Dept. 60 pp. [Processed.]

The effect of tagging on survival of fish released in the reservoir apparently varied in

different years. In 1960, the percentages of tagged and untagged fish recovered in the spawning areas were closely similar; in 1961, more untagged than tagged fish were recovered; and in 1962 the percentage recovery was higher for untagged fish than for either fin-clipped or tagged fish, and higher for fin-clipped than for tagged fish (table 2).

A high mortality of tagged fish was apparent in the early phase of the 1962 experiment. No recoveries were made of tagged fish released in the reservoir or in the Snake River during the first 4 weeks of tagging, August 27 to September 23 (table 3), and only one recovery was made from fish released in the first 5 days of the following week of tagging. This lack of tag recoveries coincided with a period of sustained high water temperature at both release sites. The average temperature of surface water was 22.1° C. (range, 21.1° to 23.9°) in Brownlee Reservoir and 18.4° C. (range, 16.6° to 20.6°) in the Snake River.

TABLE 3.—Numbers of tagged fall-run chinook salmon recovered on the spawning grounds after release above Brownlee Dam in 1962, by week of release

Week of release	Fish released in reservoir	Fish recovered on spawning grounds	Fish released in river	Fish recovered on spawning grounds
	Number	Number	Number	Number
Aug. 27–Sept. 2	11	0	7	0
Sept. 3–9	30	0	29	0
Sept. 10–16	33	0	31	0
Sept. 17–23	96	0	85	0
Sept. 24–30	74	2	46	3
Oct. 1–7	158	7	80	5
Oct. 8–14	34	3	41	2
Oct. 15–21	8	1	21	1

The high temperature, however, apparently was not the direct cause of mortality. The good recovery of untagged fish in 1962 (highest of the 3 years) suggests that a fair number of untagged fish from the early releases must have survived and reached the spawning grounds in spite of the high water temperatures. Possibly the additional stress on fish during handling, anesthetizing, and tagging produced the mortalities.

Mortality from tagging was also indicated in 1961 by the differences in percentage recov-

³ Alan B. Groves. 1963. Fishery Biologist, Biological Laboratory, Bureau of Commercial Fisheries, Seattle, Wash.

ery of tagged and untagged fish released in the reservoir. Graban (1964)⁴ observed that tagging mortality approached 30 percent. Although total recoveries of tagged and untagged fish in the 1960 experiments did not differ appreciably—possibly because of the selection of large, healthy fish for tagging—Hauck (see footnote 1) reported, “A decrease in survival (recovery) rates is indicated with increasing water temperatures at release site. . . .”

Recoveries of fish from the fin-clipped group in 1962 also give evidence of stress from handling: the percentage of returns was only about one-third that of returns from untagged salmon (table 2). The percentage of recoveries was higher from fin-clipped fish than from tagged fish (even though handling procedures were about the same for both lots), but most of the fin-clipped fish were released when water temperatures were declining and, hence, becoming more favorable for survival.

SPAWNING SUCCESS

Annual surveys by Richards⁵ and Pirtle and Keating (1955)⁶ provided percentages of totally spent fish on the spawning grounds from inspection of gonads and counts of eggs retained before and after the filling of Brownlee Reservoir in 1958 (fig. 5). These observations showed that passage through the reservoir did not affect the ability of fall-run chinook salmon to spawn successfully. The difference between percentages of totally spent fish in the preimpoundment and postimpoundment years was not significant.

Information on the use of specific areas for spawning by various salmonids was obtained from surveys before and after the impoundment was formed and from discussions with personnel of the Oregon State Game Commission, who annually surveyed spawning fish in the Powder River and its major tributary—

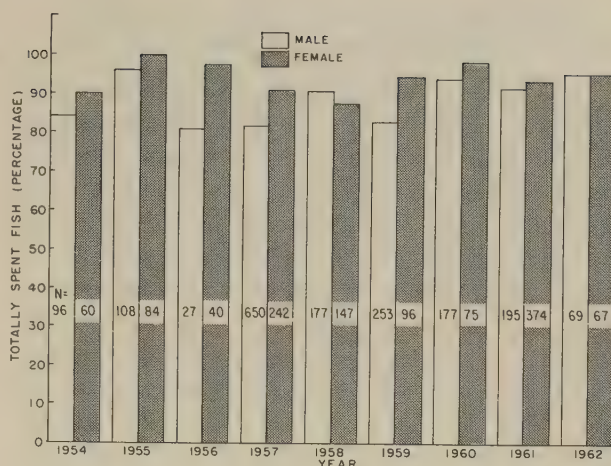


FIGURE 5.—Percentage of totally spent fall-run chinook salmon recovered on spawning ground surveys in the Swan Falls area, Snake River, 1954-62. Numerals in each bar indicate number of fish. Brownlee Reservoir was filled in 1958.

Eagle Creek; the Idaho Fish and Game Department carried out similar spawning surveys upstream from the impoundment in the Snake and Weiser Rivers. Records of State fishery agencies and of the Bureau of Commercial Fisheries on the capture of juveniles migrating from these various spawning areas also verified previous spawning.

The formation of Brownlee Reservoir apparently did not affect the ability of anadromous salmonids to use specific spawning areas. Fall-run chinook salmon passed through the impoundment after construction of Brownlee Dam and spawned in their accustomed area near Swan Falls. Because no tagged fall-run chinook salmon were observed in other spawning streams in 1960-62, straying evidently was slight or nil. Spring-run chinook salmon and steelhead trout, as evidenced by surveys on spawning grounds and by catches of their progeny in sampling traps, continued to use widely separated spawning areas after the reservoir was filled. Some spring-run populations entered the Powder River about 32 km. above Brownlee Reservoir and migrated into Eagle Creek to spawn (fig. 1), whereas others passed through the entire length of the impoundment and continued into spawning grounds in the Weiser River system.

⁴ Graban, James R. 1964. Evaluation of fish facilities, Brownlee and Oxbow Dams, Snake River. Idaho Fish and Game Department, 60 pp. [Processed.]

⁵ Richards, Monte. 1956-62. Snake River fall-chinook spawning ground surveys. Idaho Fish and Game Department. Various pagination. [Processed.]

⁶ Pirtle, Ralph B., and James Keating. 1955. Annual report: The size and timing of runs of anadromous species of fish in the Columbia and Snake Rivers and their tributaries above the confluence of the Snake River, 1954. Idaho Fish Game Dept., Contract DA 35-026-eng-20608, for U.S. Army, Corps Engrs., 30 pp. [Processed.]

RATES OF MIGRATION OF FISH MARKED WITH PETERSEN TAGS

The rate of movement of chinook salmon in Brownlee Reservoir in 1960 was estimated by Hauck (see footnote 1) from tagged fish that sport fishermen recovered on the spawning grounds. Eight fish released in the reservoir and five released in the river were recovered; the elapsed time from release to recovery averaged 32.0 days (range, 17 to 42) for fish released in the reservoir and 25.8 days (range, 18 to 30) for those released in the river 16 km. above the reservoir. On the basis of the difference between the averages (6.2 days) and the distance between the reservoir and the river release sites (104.5 km.), he estimated the average rate of movement in the reservoir as 16.8 km. per day.

Rates of migration were not studied in 1961, but in 1962 the rate of movement through the reservoir was estimated from data on five tagged fish that were identified as they migrated through a gate in a weir in the Snake River (fig. 6). The weir was 20 km. above the reservoir and 1 km. above the river release site, which was 19 km. above the reservoir in 1962. (Midway through the experiment, it became evident that the weir was delaying upstream migration; the structure was removed at the end of September to allow free passage of adult



FIGURE 6.—Snake River weir (upstream view) with fish traps for identification and release of migrating salmon. Site is about 20 km. above Brownlee Reservoir.

migrants.) The total elapsed time between release of the five fish above Brownlee Dam and recapture at the weir (108.5 km. upstream) ranged from 3.2 to 9.9 days and averaged 6.7 days. Thus, the average rate of upstream movement from release to passage through the weir was 16.1 km. per day. The true rate of movement may have been somewhat faster than indicated because the calculation does not take into account any possible delays at the weir.

Thirteen tagged salmon released in the Snake River in 1962 were observed passing through the weir, 1 km. upstream, in elapsed time that ranged from 2.2 hours to 6.6 days and averaged 2.8 days (or about 0.36 km. per day). The delaying effect of the weir undoubtedly accounted for the low rate of movement in this stretch of river. As is shown in the next section, more than half of the sonic-tagged fish reached the weir in less than 1 hour; hence, they moved up this short section of stream at about 19 km. per day.

ORIENTATION AND MOVEMENT OF SONIC-TAGGED FISH

Because the sonic tags we used transmitted identifiable signals for only about 5 days, our experiments were limited to a study of initial behavior after release. In such a study, it is essential that the attachment of the tag not affect the behavior of the fish. We were unable to detect any immediate effect of the tag from visual observations of tagged and untagged fish released in the same area. Although the long-term effect on behavior is unknown, previous work by the Bureau of Commercial Fisheries during the past 10 years suggests that the effect may be slight (Johnson, 1957).

BROWNLEE RESERVOIR

Most of the chinook salmon with sonic tags released in Brownlee Reservoir in 1961 were initially disoriented and spent considerable time in the lower end of the reservoir before resuming migration upstream. The movement

of an obviously disoriented fish is shown in figure 7. A track of one fish that resumed migration upstream soon after release is shown in figure 8.

The initial aimless wandering of most of the sonic-tagged fish may also have been characteristic of untagged fish released in the reservoir; if so, they eventually recovered because a high percentage of fish arrived on the spawning grounds from releases in the reservoir. In 1962, for example, nearly 25 percent of the untagged fish released in the reservoir were recovered in the spawning areas. In view of the size of the Snake River (flow more than 365 c.m.s.) and the extent of spawning grounds (over 25 river km.), we can be certain the percentage of fish that reached the spawning grounds was far greater than the percentage recovered.

SNAKE RIVER

More than half of the 44 fish with sonic tags that were released in the Snake River covered the 1.0 km. stretch to the weir in less than an hour. Other fish moved more slowly. A few fish remained in the release area up to 24 hours, and one stayed 4 days before moving upstream. Only one fish moved downstream; this salmon drifted 2.4 km. below the release site, lingered about 2 hours, and then resumed its migration

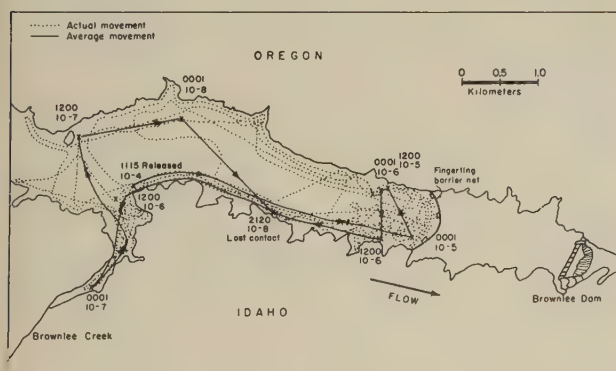


FIGURE 7.—Disoriented movement of an adult chinook salmon tagged with a sonic tag and released in Brownlee Reservoir. This fish, tracked for 106 hours, moved almost continuously day and night and traveled about 81 km. Travel was confined to area within 3.2 km. of the release point.



FIGURE 8.—Chronological record (diagrammatic) of a 77-hour track of well-oriented adult chinook salmon moving 81 km. upstream in Brownlee Reservoir. Fish carried a sonic tag.

upstream. Distributions that show the delay-effect of the weir are given in figure 9.

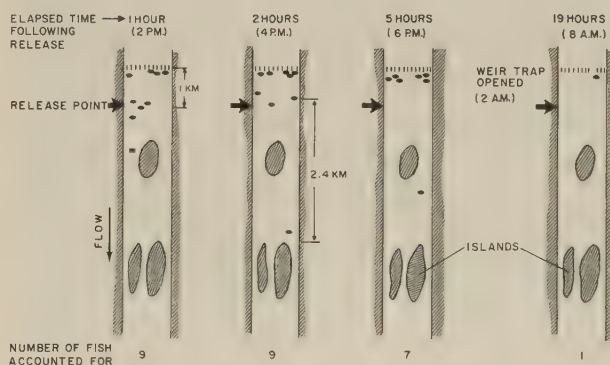


FIGURE 9.—Diagram of the changing distribution of a group of nine chinook salmon tagged with sonic tags and released in the Snake River above Brownlee Reservoir. Two fish presumably passed through the weir between 4 and 6 p.m. No fish were found farther than 2.4 km. downstream from the weir.

In a similar, earlier release from the same site, all but one of seven fish moved up to the weir during the afternoon. Some fish then dropped downstream about 1 km. after dark but returned to the weir in the morning, at which time only two were counted through the gates. In three releases (total of 25 fish) after the weir was removed, the fish moved past the vacated site without hesitation.

Sonic tags provided additional information on rates of movement in the river. Fish took from 26 to 120 hours to move upstream from the release point to the monitor at the Payette River mouth, which was 24 km. upstream. The maximum rate of movement for the distance was, therefore, slightly more than 0.8 km. per hour, or 19 km. per day. The slowest fish recorded by the monitor moved 13 km. upstream in 6 days; this was the same fish mentioned earlier, which had spent 4 days in the release area before resuming migration.

EXAMPLES OF PASSAGE THROUGH LARGE NATURAL LAKES

Because Brownlee Reservoir provides the only evidence of chinook salmon passage through a long, deep impoundment, we searched for other examples of their passage capabilities under comparable conditions. Passage of chinook salmon through large, shallow impoundments, such as those formed by low-head dams on the Columbia River, has long been established. These impoundments pass tremendous volumes of water and normally provide strong directional currents that are usually absent in large, deep reservoirs, such as Brownlee. What was needed were examples of passage through large bodies of water having low or no directional currents. Although large lakes with inlets and outlets may differ from reservoirs, the flow of water and limnological conditions can be similar to those in large, deep impoundments.

We discussed the passage of adult chinook salmon through large, natural bodies of water with biologists familiar with chinook salmon runs in Alaska, British Columbia, and the Yukon Territory. They estimated the sizes of

sustained runs and provided data on the sizes of lakes through which the species migrates to reach spawning areas.

We concluded that the size of a body of water may not influence greatly the upstream migration of this species. In Bristol Bay, Alaska, chinook (king) salmon have been observed in the upper Wood River Lakes (Burgner, personal communication⁷). To reach this area, the fish migrate through three connecting lakes—about 30 km. through Aleknagik Lake, about 56 km. through Lake Nerka, and about 24 km. through Lake Beverly. An average of 5,000 adults entered in 1957–62 and spawned in tributaries to Naknek Lake (about 64 km. long) (Jaenicke, personal communication⁸). Some of these fish were observed at the Brooks Lake weir in a tributary stream about 48 km. above the outlet of Naknek Lake.

In British Columbia (Fraser River system), researchers⁹ estimated that 500 to 1,000 adult chinook salmon pass through Harrison Lake (80 km.) into the Birkenhead River; about 5,000 migrate through Kamloops Lake (24 km.) and continue for 72 km. through Shuswap, Eagle, and Mara Lakes to spawn. Some chinook salmon pass 72 km. through Quesnel Lake into the Mitchell River. Before Coulee Dam was constructed on the Columbia River, large runs of chinook salmon were reported by local residents (Bryant and Parkhurst, 1950) to have migrated through the lower Arrow Lake (72 km.) and upper Arrow Lake (56 km.) to spawn below Windermere Lake, 128 km. farther upriver.

More than 3,600 chinook salmon are estimated by Elliott (personal communication¹⁰) to enter LaBerge Lake on the Yukon River, Yukon Territory. A small number enter a tributary about halfway through the 56-km. lake, but most continue through the lake to the Takhini and McKlintock Rivers. Another run

⁷ Robert L. Burgner. 1963. Fisheries Research Institute, University of Washington, Seattle, Wash.

⁸ Herbert W. Jaenicke. 1964. Fishery Biologist, Bureau of Commercial Fisheries, Auke Bay, Alaska.

⁹ J. R. Brett, Fishery Research Board of Canada, Nanaimo, B. C.; and W. R. Hourston, D. McKinnon, and B. M. Chatwin, Department of Fisheries, Canada, Vancouver, B. C.

¹⁰ W. K. Elliott. 1964. Fishery Officer, Department of Fisheries, Canada, Whitehorse, Yukon Territory.

of 2,000 fish migrate up the Teslin River, tributary to the Yukon River below LaBerge Lake, and continue 72 km. into Teslin Lake before entering the Nisutlin River; from here the fish continue for another 153 km. to a spawning area at the outlet of Nisutlin Lake.

IMPLICATIONS OF PRESENT RESEARCH

Our experiments indicated that adult fall-run chinook salmon can migrate through large impoundments. This ability apparently does not require previous reservoir experience in the juvenile stage; adult salmon returning upstream through Brownlee Reservoir in 1958-60 had passed downstream through this area as juveniles when it was still a river. The results point to the feasibility of passing adult chinook salmon directly through large storage reservoirs, thus eliminating the need for extended transport around impoundments.

The successful passage of fall chinook salmon through Brownlee Reservoir has special significance because the environment for the survival of upstream migrants is perhaps as poor as any found in the present freshwater range of this species. Surface temperatures over 21° C. are common in the reservoir until mid-September, and oxygen concentrations in the deeper, cooler water generally are 4 p.p.m. or less¹¹ during the fall migration. Despite the marginal environment for survival of salmonids in the reservoir, adult migrants apparently suffered no greater losses than the fish bypassed upstream to the river, where water temperatures and oxygen concentrations were much more favorable.

¹¹ Ebel, Wesley J., and Charles H. Koski. Physical and chemical limnology of Brownlee Reservoir. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash. Manuscript in preparation.

CONCLUSIONS

The studies on chinook salmon in the Brownlee Reservoir area support the following conclusions:

1. Evidence of successful passage by chinook salmon through Brownlee Reservoir and of their sustained migration through large lakes in Alaska, British Columbia, and Yukon Territory suggests that the large size of an impoundment may not be detrimental to upstream migration of this species.

2. Despite initial disorientation, chinook salmon released in the reservoir were able to reach spawning areas as successfully as those transported and released in the river above the impoundment. In the river, fish resumed migration shortly after release.

3. The ability of fish to spawn successfully was not affected by passage through the reservoir.

4. Ancestral spawning grounds in the Snake River above the reservoir continued to be used after the impoundment was formed.

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DISTRIBUTION, APPARENT ABUNDANCE, AND SIZE COMPOSITION OF ALBACORE (*THUNNUS ALALUNGA*) TAKEN IN THE LONGLINE FISHERY BASED IN AMERICAN SAMOA, 1954-65

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ABSTRACT

This fishery began in 1954 when tuna canning began in Pago Pago, American Samoa, with fish delivered by seven Japanese longline vessels. The size of the fishing fleet grew rapidly. In 1963, a second cannery began operating in Pago Pago. The 105-vessel fleet fishing during the last quarter of 1965 had 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China. The fishery was close to the Samoa Islands in the early years but expanded rapidly to the east and south; in 1965 it covered an area of about 23 million square kilometers (6.7 million square nautical miles) in the central and eastern South Pacific Ocean.

Albacore is fished selectively by the fleet because it commands the highest prices at the canneries. Data from the American Samoa-based fishery are complete, therefore, only for the albacore catches. Data on the

other tuna species are not analyzed. The landings of albacore in American Samoa have increased from 338 metric tons in 1954 to 15,588 metric tons in 1965. In general, the annual landings have tended to be directly proportional to the total amount of fishing effort.

Various indices of apparent abundance of albacore (catch per trip, catch per day, and catch per 100 hooks fished) are examined. The catch per unit of effort in 1954-65 showed relatively little change in terms of numbers of fish, but a rather marked downward trend in terms of weight. This decline was due largely to a decrease in the average size of the albacore. Among the possible causes for the decrease in fish size are (1) fishing ground selection, (2) decrease of older, larger fish in the stock due to fishing and natural mortalities, (3) entry into the fishery of an abundant year class, and (4) change in sex ratio of the albacore taken.

Before World War II there was almost no long-line fishing for tuna in the South Pacific Ocean. After the ratification of the Peace Treaty in April 1952, the South Pacific Ocean became accessible to the Japanese. They started fishing in the western South Pacific near the Solomon Islands, principally for yellowfin tuna (*Thunnus albacares*). The Japanese sent fishing expeditions to waters as far south as lat. 15° S. in late 1952 and extended fishing to lat. 25° S. in the western South Pacific Ocean in 1953 and 1954 (personal communications, Nankai Regional Fisheries Research Laboratory, Kochi, Japan).

In 1954, the tuna fishery based in American Samoa began with a small fleet of Japanese long-line vessels. A base was also established by the Japanese at Espiritu Santo in the New Hebrides

in 1958 and in the Fiji Islands in 1963. Many independently operated vessels, without the support of foreign land bases or of mother ships, are fishing in the South Pacific and landing their catches of tunas and billfishes directly in Japanese ports. Unquestionably, fishing effort in the South Pacific Ocean has increased substantially over the last decade.

The fishery was conducted exclusively by the Japanese in the early years, but, beginning about 1958, more and more vessels from the Republic of Korea and the Republic of China have been participating. The Japanese early discovered the value of albacore (*T. alalunga*) as a high-quality export product. Since 1956 most of the fishing effort of the American Samoa-based fleet has been concentrated on albacore rather than yellowfin tuna.

This paper describes the American Samoa-based fishery, gives biological data (size and sex) on albacore, and presents results of some preliminary analyses of the catch rates (catch per unit of effort) of albacore as a measure of apparent abundance. The exact amount of fishing effort expended by the American Samoa-based vessels relative to the total longline fishing effort in the South Pacific Ocean is not known. Although no reliable estimates are available, it is apparent that the relative effort changes from year to year. Apparently, the American Samoa effort decreased progressively in relation to the total South Pacific fishing effort from 1954 at least through 1962. Because of this, we have incorporated data from Japan-based longline vessels fishing in the same general area, wherever possible, to supplement the data collected from American Samoa.

In late 1962 the BCF (Bureau of Commercial Fisheries) Biological Laboratory, Honolulu, began to record the size and sex of albacore landed in American Samoa. Because of the rapid growth of the longline fishery we decided to attempt to follow the effects of the fishery on the resource by also collecting catch and effort statistics. In April 1963 a field station, manned by personnel from the BCF Biological Laboratory in Honolulu, was established in Pago Pago, American Samoa, to conduct intensive sampling of the fishery.

Data are collected both on the biology of the albacore landed at the canneries and on fishing operations as recorded by the vessel operators. The length, weight, and sex of 50 albacore, randomly chosen, are being obtained from each trip landing. Detailed catch and effort data are provided voluntarily by fishing vessel operators. The cooperation of vessel operators has been gratifying; data are returned from about 85 percent of the fishing trips. These data provide information on the daily fishing effort (number of hooks fished per set) as well as the catch in numbers of the various species.

THE AMERICAN SAMOA-BASED FISHERY

The past two decades have seen the establishment of two tuna canneries in American Samoa. In 1949, a small tuna cannery was installed on the north shore of Pago Pago Bay on Tutuila Island, American Samoa, by Island Packers, Inc. Attempts to supply this cannery with tuna by live-bait fishing and purse seining in Samoan waters

failed, and the plant never operated. The Government of American Samoa, owner of the land and the buildings, purchased the cannery equipment to prevent its being dismantled and sold abroad. In 1953, the Van Camp Sea Food Company obtained a lease with a renewal option (Van Campen, 1954). Today, the tuna cannery, much improved by the installation of new equipment and modernized facilities, is being operated by the Van Camp Sea Food Company-Samoa. In the latter part of 1963, Star-Kist Samoa, Inc. began operating a new cannery adjacent to the Van Camp plant.

The two canneries depend entirely upon foreign flag vessels and fishermen for their catch. Vessels from Japan, the Republic of Korea, and the Republic of China are placed under contract for specified periods, either directly with vessel owners or more generally through fishing companies, to deliver their catches to these American tuna canneries.

The fish are caught by longlines in the South Pacific in an extensive area covering 23 million square kilometers; the 1965 fleet of 154 vessels landed 15,588 metric tons of albacore and lesser quantities of other pelagic species. The following sections give details on the fishing method, fishing grounds, the fleet, and the fish landings.

FISHING METHOD

The American Samoa-based vessels fish with longlines (fig. 1). The basic unit of longline gear ("basket") consists of a length of mainline 200 to 400 m. long, from which are suspended branch lines (usually five or six) with baited hooks. The mainlines are buoyed to the surface by float lines. About 300 baskets of gear are joined in a series. The gear, thus, extends about 100 km. in a single fishing operation. In 1965, the vessels from American Samoa fished an average of 1,400 hooks in a single set. A fishing operation requires upward of 20 to 22 hours from the time the gear is set (about 0400 hours) until it is completely retrieved (about 0100 the following morning).

FISHING GROUNDS

The geographical expansion of the fishery is illustrated in figure 2. In the early years the fishery was confined largely to the vicinity of the Samoa Islands, but the vessels have gradually extended their operations to more distant waters. By 1956,

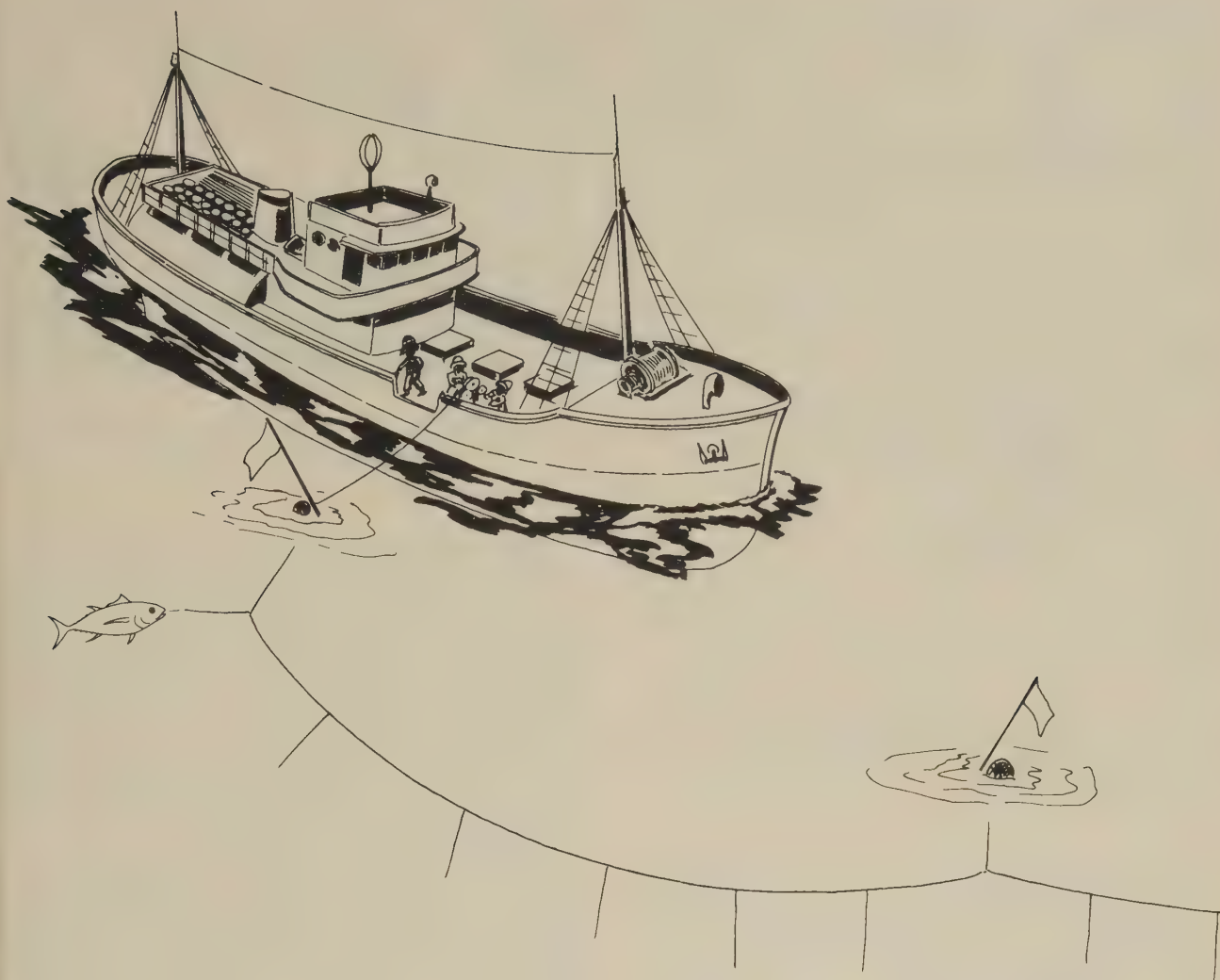


FIGURE 1.—Schematic representation of the longline fishing method used in the American Samoa-based fishery.

considerable fishing had already taken place as far south as lat. 28° S., in waters southeast of the Tonga Islands. The greatest expansion of grounds was in 1958, however, when vessels extended fishing eastward to the Marquesas Islands. In 1965, the vessels fished in an extensive area from the Equator to lat. 30° S. and from about long. 175° E. to about long. 120° W., an area of about 23 million square kilometers (6.7 million square nautical miles). Vessels have fished as far as 5,500 km. (3,000 nautical miles) from their base.

FISHING FLEET

Beginning in 1954 with 7 fishing boats contracted from Japan (a total of 16 different vessels

participated in the fishery for varying periods during the year), the fleet in American Samoa has continued to increase over the years (fig. 3). Despite year-to-year fluctuations, the trend has been one of rapid increase; in 1965, 154 different vessels fished from American Samoa. The tremendous increase in fleet size in 1963 reflects the start of operations that year of the Star-Kist tuna cannery.

The composition of the fishing fleet, in terms of the country of origin of the vessels, has changed over the years. In the early years of the fishery, the entire fleet was Japanese. Vessels from the Republic of Korea began operating in the area in 1958 and vessels from the Republic of China in

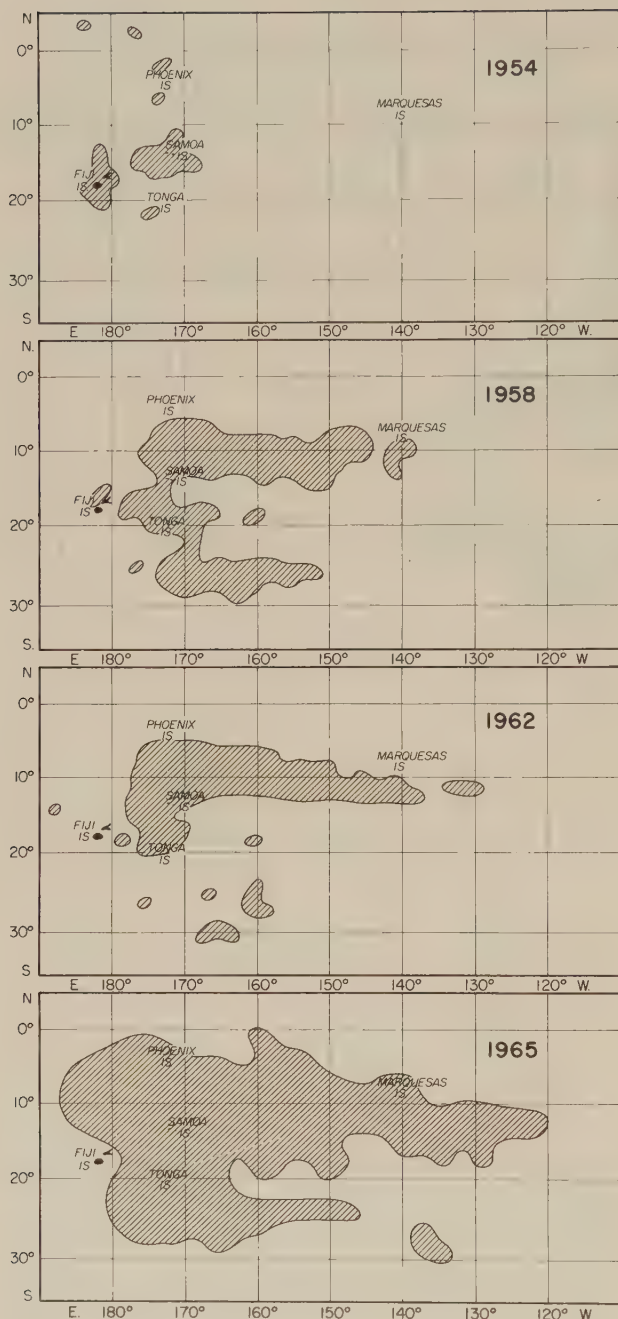


FIGURE 2.—Geographic expansion of fishing grounds of American Samoa-based vessels, 1954–65.

1964 (fig. 3). The 105-vessel fleet operating during the last quarter in 1965 had 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China.

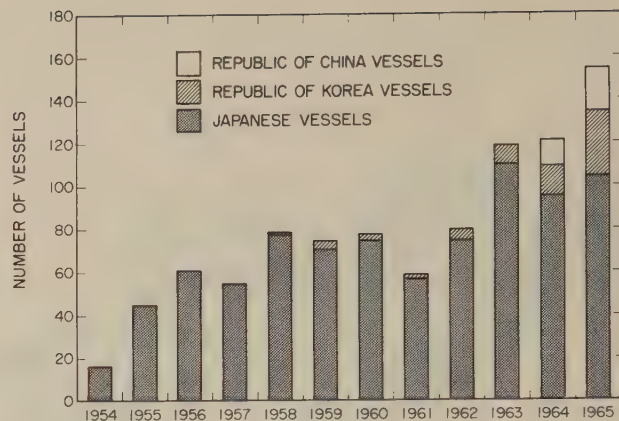


FIGURE 3.—Number of vessels in the American Samoa-based longline fishery, 1954–65.

SPECIES COMPOSITION OF THE LANDINGS

Albacore commands the highest price at the cannery and is, consequently, fished for selectively by the fleet. This selection occurs both by the choosing of areas in which albacore are most plentiful instead of areas with the greatest combined species catch and (on occasion) by the discarding of other species caught to conserve storage room for more albacore. Thus, the albacore catch alone is delivered in its entirety to the cannery.

Yellowfin tuna constitutes the second most important species delivered to the canneries, but makes up only about 15 percent of the weight of fish landed. Other species taken by the fishery include the bigeye tuna (*T. obesus*), southern bluefin tuna (*T. maccoyi*), skipjack tuna (*Katsuwonus pelamis*), wahoo (*Acanthocybium solandri*), and various billfishes, sharks, and other pelagic species. Because catches that are not kept for delivery are often not recorded, no reliable data are available on the apparent abundance of species other than the albacore.

ANNUAL AND SEASONAL LANDINGS OF ALBACORE¹

The albacore landings by the American Samoa-based fleet have gradually increased from 338 metric tons in 1954 to 15,588 metric tons in 1965 (fig. 4). The upward trend was broken in 1961 and 1964, when landings smaller than those of the pre-

¹ Catch statistics in this report are based on dates of capture and may not agree with figures previously reported from this fishery, which were based on dates of delivery.

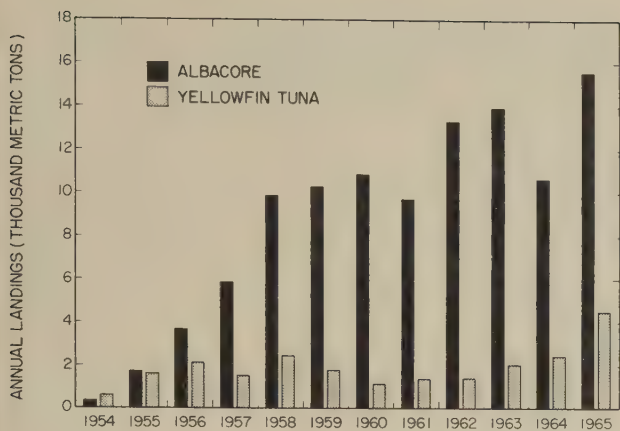


FIGURE 4.—Total annual albacore and yellowfin tuna landings in American Samoa, 1954–65.

ceding year were registered. Although yellowfin tuna was the dominant species landed in 1954 and in parts of 1955 and 1956, the albacore has dominated the catch since 1957.

Albacore are taken throughout the year (fig. 5). In most years for which we have data, slightly better landings have been made during the latter half of the year. In some years (e.g., 1961, 1963, 1964), however, no seasonal trend is evident.

APPARENT ABUNDANCE OF ALBACORE

Various indices of apparent abundance of albacore are examined in the following sections. These include catch per trip, catch per day, and catch per 100 hooks fished.

CATCH PER TRIP AS A MEASURE OF APPARENT ABUNDANCE

The apparent abundance of tunas taken by a longline fishery is generally measured by the catch per 100 hooks fished. We did not, however, begin to collect information on the number of days fished per trip until 1959 and did not begin to collect data on the number of hooks fished per day until 1963. We were compelled, therefore, to use the fishing trip itself as the unit of effort to indicate trends in apparent abundance of albacore for the entire period of existence of the American Samoa-based fishery.

Admittedly, the catch per trip is an inexact measure of apparent abundance because it is greatly influenced by changes in number of days fished

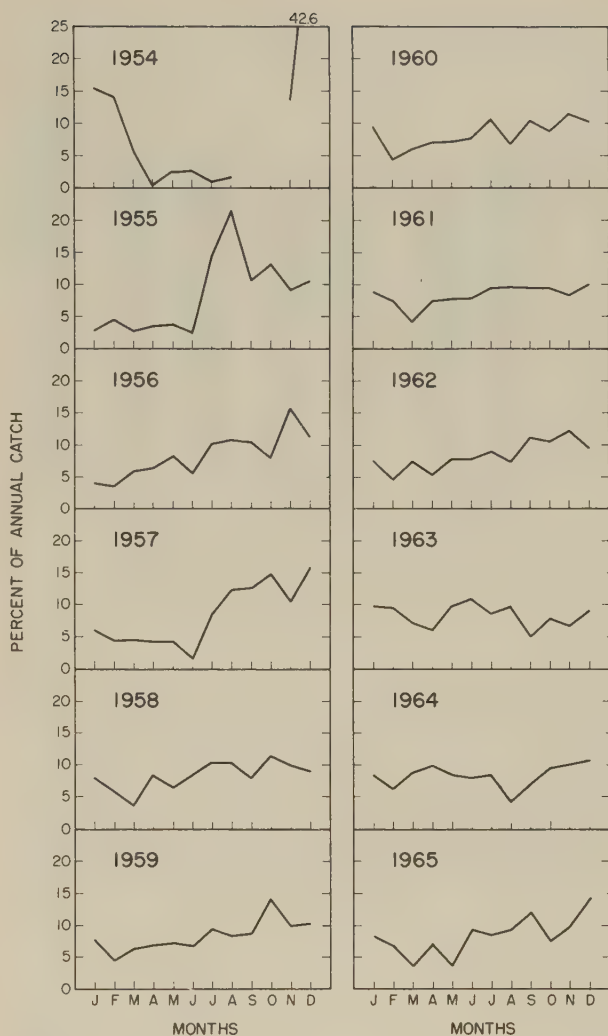


FIGURE 5.—The monthly catch of albacore, in percentages of annual total, by American Samoa-based vessels, 1954–65.

per trip and by size composition of vessels in the fleet. The average number of days fished per trip by the American Samoa-based vessels has, however, remained relatively steady from year to year, at least between 1959 and 1964 (fig. 6). As we show later, size composition of vessels also changed little during the entire 1954–65 period. Furthermore, the close relation between the monthly average catch per trip and the monthly average catch per day fished, assuming that catch per day is a more reliable index (fig. 7), indicates that the catch per trip is a satisfactory measure of apparent abundance.

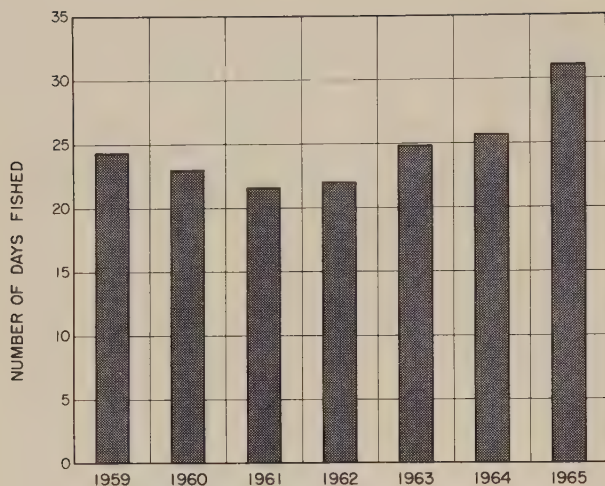


FIGURE 6.—Average number of days fished per trip by vessels based in American Samoa, 1959–65.

In figure 8 are shown the total number of fishing trips and the average catch of albacore per fishing trip, along with the annual landings of albacore, for 1954–65. Annual landings have fluctuated with fishing effort. Between 1958 and 1960, however, landings increased despite a decrease in fishing effort. This increase was due to increased average

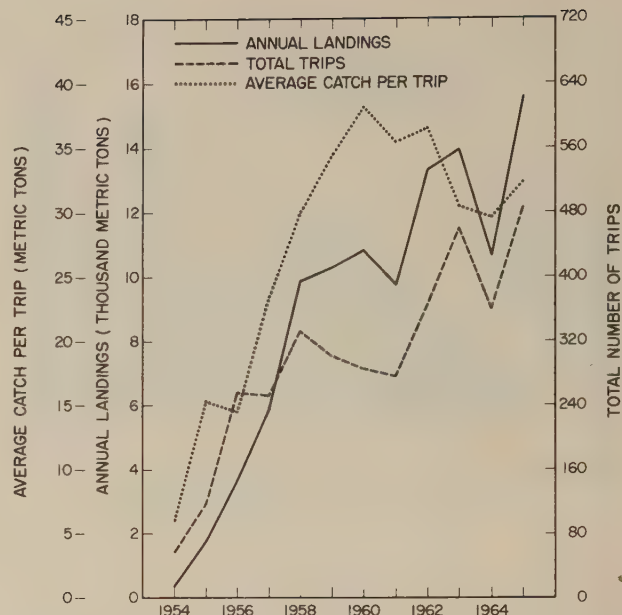


FIGURE 8.—Total annual number of fishing trips, average catch of albacore per trip, and annual albacore landings, by American Samoa-based vessels, 1954–65.

catch of albacore per trip during the period. The rather sharp decline in landings in 1964 resulted from the combined effects of a decrease in average catch per fishing trip and a drop in fishing effort.

From 1954 through 1960 the catch per trip increased, then tapered off and stabilized at a lower level in 1963–64, and finally increased slightly in 1965. The upward trend in 1965 was attributable primarily to the increased length of the average trip (fig. 6). The catch per trip, in metric tons, averaged 35.7 in 1961–62, 30 in 1963–64, and 31.6 in 1965.

The total annual landings declined in 1964 although the size of the fleet had increased since 1963. The number of fishing trips, however, declined sharply, from 451 to 359, and the average number of days fished per trip increased only slightly, from 24.9 to 25.7 days.

The Japan Fisheries Agency (1966), in its publication of the 1963 Japanese tuna longline data, pointed to a rather marked decline in albacore catch rates throughout the South Pacific Ocean during 1963, with the possible exception of the “newer” grounds east of long. 130° W. (table 1). It noted that although fishing effort had increased 16 percent, from 58.2 million hooks fished in 1962

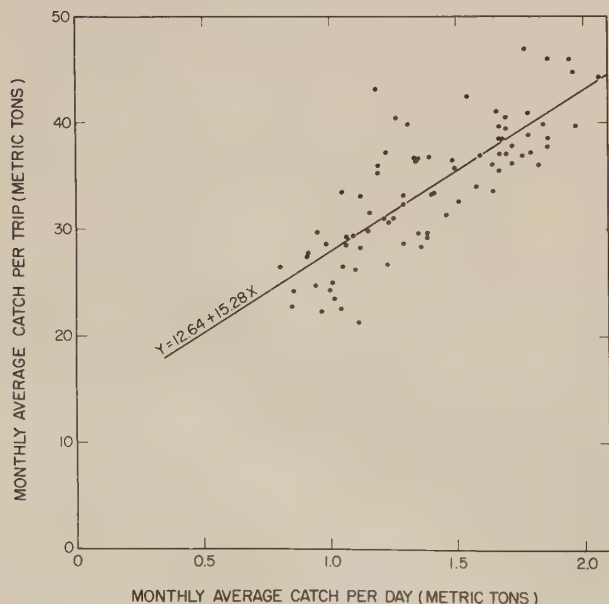


FIGURE 7.—Relation between monthly average catch of albacore per trip and monthly average catch per day by American Samoa-based vessels, 1959–65.

to 67.7 million in 1963, the catch of albacore had decreased 14 percent, from 2.1 million fish to 1.8 million. For example, in the western South Pacific between long. 150° E. and 180°, the catch rates decreased from 3.1 albacore per 100 hooks in 1962 to 1.9 in 1963, and in the central South Pacific (between 180° and 130° W., corresponding to the fishing grounds of the American Samoa-based vessels) the decrease was from 4.6 to 3.1 albacore per 100 hooks. Unlike the relatively low catch rate of 3.1 reported by the Japanese for 1963, our data from American Samoa-based vessels show an average of 4.9 albacore per 100 hooks for the year (fig. 9). This difference may possibly be attributable to a greater degree of selectivity for albacore on the part of the American Samoa-based vessels. The decrease in 1963, pointed out by the Japanese, is, however, paralleled by a similar decrease in our data on catch per trip beginning early in 1963.

TABLE 1.—*Japanese data on catch and effort for albacore in the South Pacific Ocean, 1962 and 1963*

[This table is based on table 10, Japan Fisheries Agency, 1966]

Fishing area	Number of hooks		Number of albacore		Catch per 100 hooks	
	1962	1963	1962	1963	1962	1963
	<i>Mil-</i>	<i>lions</i>	<i>Thou-</i>	<i>sands</i>	<i>Num-</i>	<i>Num-</i>
	<i>lions</i>		<i>sands</i>		<i>ber of</i>	<i>ber of</i>
					<i>fish</i>	<i>fish</i>
Long. 150° E.-180° Lat. 10°-30° S.	27.7	17.9	846.2	333.1	3.1	1.9
Long. 180°-130° W. Lat. 5°-30° S.	25.6	32.0	1,167.3	997.3	4.6	3.1
Long. east of 130° W. Lat. 10°-30° S.	4.9	17.8	122.3	437.7	2.5	2.5
Totals.....	58.2	67.7	2,135.8	1,768.1	3.7	2.6

Catch per 100 hooks is an index of apparent abundance in terms of numbers of fish, whereas catch per trip is measured in terms of weight of albacore taken. The decrease in the latter index in 1963, 1964, and part of 1965 was caused in large part by a decrease in the average size of albacore. Though fluctuating greatly, the catch in numbers per 100 hooks from 1963 to 1965 did not show a marked downward trend. On the other hand, the same data, converted into catch in weight per 100 hooks (by using the monthly mean weight of albacore sampled from the fishery), showed a decreasing trend through 1965 (fig. 9). Several possible causes for the observed decrease in the size of the fish are discussed later.

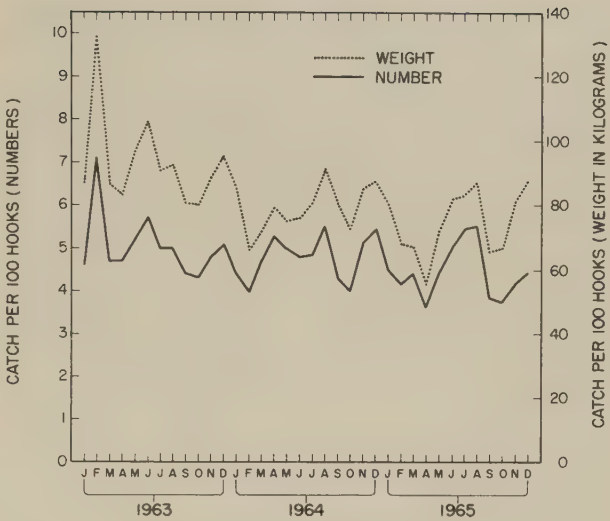


FIGURE 9.—Catch of albacore per 100 hooks, in numbers and in weight, by the American Samoa-based vessels, 1963-65.

RELATION BETWEEN CATCH AND EFFORT

The relation between annual total landings of albacore and total fishing effort (number of fishing trips) shown in figure 10, though seemingly linear, needs to be interpreted with caution, be-

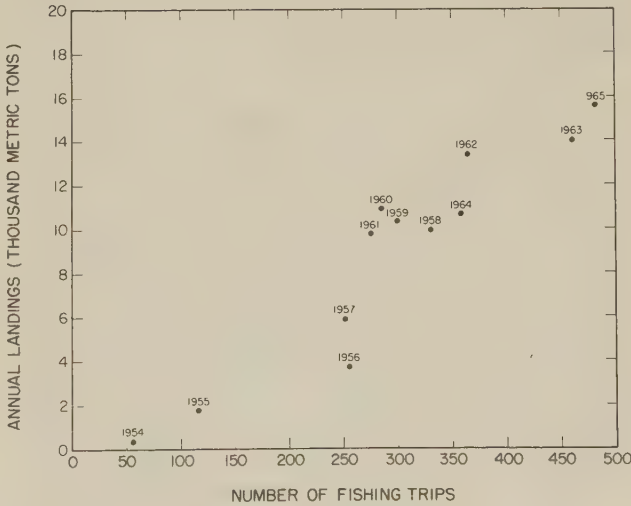


FIGURE 10.—Relation between annual total landings of albacore and total fishing trips of American Samoa-based vessels, 1954-65.

cause the data for the earlier years—particularly 1954 and 1955—are not strictly comparable with those of later years. As we already stated, fishing in the early stages of the fishery was aimed primarily at taking yellowfin tuna rather than albacore; thus, the catch of albacore per fishing trip was relatively small as compared with later years.

It is clear, however, that the annual landings of albacore have tended to increase with increasing fishing effort. Generally, it would be expected that the total catch would increase as fishing effort increases, until a point of maximum yield (not necessarily the point of optimum yield) is reached. After this point is reached, the catch would generally decrease despite further increase in effort. From the data presented in figure 10, it does not seem that the point of maximum yield of albacore has yet been reached in the American Samoa-based fishery. The extent of the growth potential, however, is a subject of another study—one which will require the analysis of all available South Pacific data, not merely those collected from the American Samoa-based vessels.

RELATION BETWEEN CATCH PER UNIT OF EFFORT AND EFFORT

The annual average catch per trip shows an apparent increase with increase in fishing effort (fig. 11). The catch per trip in 1963, 1964, and 1965, however, failed to increase at the rate seen before 1962. The data are far too few, however, to be conclusive.

VALIDITY OF CATCH PER 100 HOOKS AS MEASURE OF APPARENT ABUNDANCE

Under the assumption that the catch per 100 hooks is the better measure of apparent abundance of a species taken by the longline method, such data have been collected continuously since 1963. Estimates of abundance of fish based on catch per day or catch per trip might be influenced by the size of the fishing vessel. Although there seems to be no reason for believing that catch per 100 hooks would also be affected by vessel size, this question was examined inasmuch as it is conceivable that the larger vessels may be more attractive to fishermen than smaller vessels and,

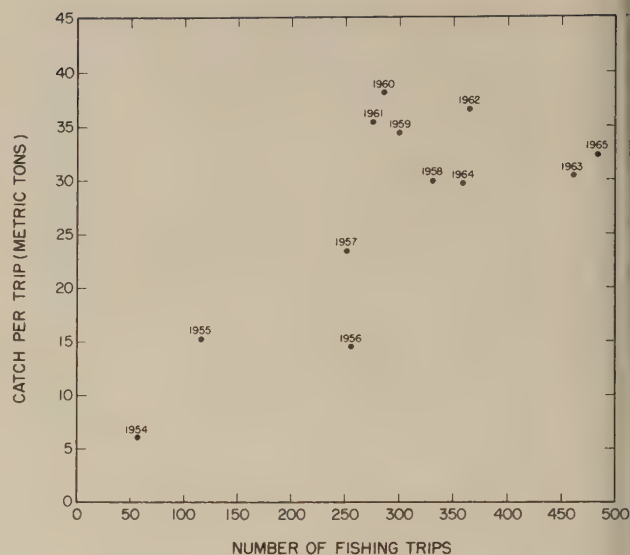


FIGURE 11.—Relation between average catch of albacore per trip and total fishing trips, of American Samoa-based vessels, 1954–65.

thus, may have a better choice of fishermen and fishing masters who would have the skill to catch more fish. If so, some efficiency factors would need to be incorporated in the use of catch per 100 hooks to adjust for differences among vessels.

A tabulation of albacore catch per 100 hooks by vessel sizes (gross tonnage) revealed a tendency for larger vessels to obtain higher catch rates than smaller vessels (table 2). In 1963, the smallest vessels (under 80 gross tons) averaged 4.6 albacore per 100 hooks, but catches trended upward to 5.8 albacore per 100 hooks for the vessels of 121 to 140 tons. The average catch rate was lower (5.1) for the largest vessels (those over 141 gross tons). In 1964, the trend, if any existed, was less obvious. To examine this apparent relation between vessel size and catch rate, the catch rate for each trip was plotted against vessel size for each of the 24 months. The scatter of points about the regression lines, fitted by the least squares method, was considerable; only the data for June and November 1963 and September 1964 showed statistically significant regressions ($P < 0.01$). The data for these 3 months, however, were very heavily influenced by the results of a disproportionately small number of both the smallest and largest vessels in the fleet.

TABLE 2.—*Catch rates and fishing effort of American Samoa-based vessels¹ by vessel size groups, 1963 and 1964*

Item	Vessel size (tons)				
	<80	81-100	101-120	121-140	>141
Catch of albacore per 100 hooks:					
1963.....	4.6	4.9	5.1	5.8	5.1
1964.....	4.9	4.7	4.8	5.4	4.4
Number of fishing trips:					
1963.....	68	266	44	24	21
1964.....	23	171	59	27	36
Percentage of fishing trips:					
1963.....	16.1	62.9	10.4	5.7	5.0
1964.....	7.3	54.1	18.7	8.5	11.4

¹ Vessel-size data were not available for all vessels.

The higher average catch rates achieved by the larger vessels (121-140 gross tons) in 1963 and 1964, were probably due to the skill of the fishing master in selecting productive fishing grounds, or to subtle differences in fishing techniques rather than to vessel size alone. For example, the high average catch rate of 5.8 albacore per 100 hooks in 1963 was achieved by only six vessels, which rather consistently made good catches. One large vessel fished 2 months in 1963 with poorer than average results, but this vessel apparently left the American Samoa fishery soon thereafter.

Furthermore, the excellent performance of some of the smaller vessels also argues strongly against dependence of catch rates upon vessel size. A 60-ton vessel, for example, attained higher than average catch rates in 6 of the 9 months during 1963; its annual mean catch rate was 5.3 albacore per 100 hooks as compared with the average of 4.6 achieved by all vessels smaller than 80 gross tons.

It is, therefore, reasonable to conclude that catch rates (catch per 100 hooks) are not influenced by vessel size, and that they are valid indices of the apparent abundance of albacore.

Although catch per day's fishing and catch per trip tend to increase with size of vessel, the fact that relatively few vessels in the fleet were larger than 120 tons or smaller than 80 tons enabled us to use average catch per trip as a gross index of apparent abundance for years in which data on catch per 100 hooks are not available. Fortunately, a very large proportion of the vessels in the American Samoa fleet has been those of about 100 tons during the period of this study.

SEASONAL AND GEOGRAPHIC VARIATIONS IN CATCH PER 100 HOOKS

The Nankai Regional Fisheries Research Laboratory (1959) has published charts of the average monthly albacore catch rate in each 1-degree square area fished in the Pacific and Indian Oceans by using all data available through March 1956. These charts are widely used today as representative of catch rates under average conditions. Koto (1966) published the average year's catch rates of albacore in the South Pacific Ocean by summarizing data obtained from the Japanese tuna longline fishery between January 1950 and December 1961. Many of the data from the American Samoa-based fishery are missing from both the above publications. For this reason and to make possible examination of the data for any time trends in catch per unit of effort, more recent data collected from the American Samoa-based vessels are presented in figures 12-14. The catch rates (catch of albacore per 100 hooks) have been averaged by quarterly periods for 1963, 1964, and 1965 and plotted by 2-degree square areas.

These charts depict the shifting of the fishing grounds during the year. The vessels from Samoa tend to fish north of lat. 20° S. during the first and second quarters, although a few vessels venture farther south to about lat. 28° S. Vessels tend to scatter widely beginning about June or July, and many boats fish between lat. 25° and 30° S. The southern grounds are heavily fished during the latter part of the year. In general, the fishing grounds are in the north during the first half of the year, and both north and south during the second half. This situation probably holds true in most years and may reflect the movements of albacore in the South Pacific Ocean. Interviews with fishermen indicate that catch rates in northern waters are more favorable during the early months of the year. Suzuki (1961), in recording his observations on the Samoa fishing operations in 1956, attributed the seasonal shifts in fishing grounds to movements of fish. He observed that most of the vessels fished in the vicinity of lat. 27° S. in August and September and then followed the northward movement of the fish.

Seasonal and geographical differences in catch rates are not readily evident from these charts. High catch rates (more than five albacore per 100

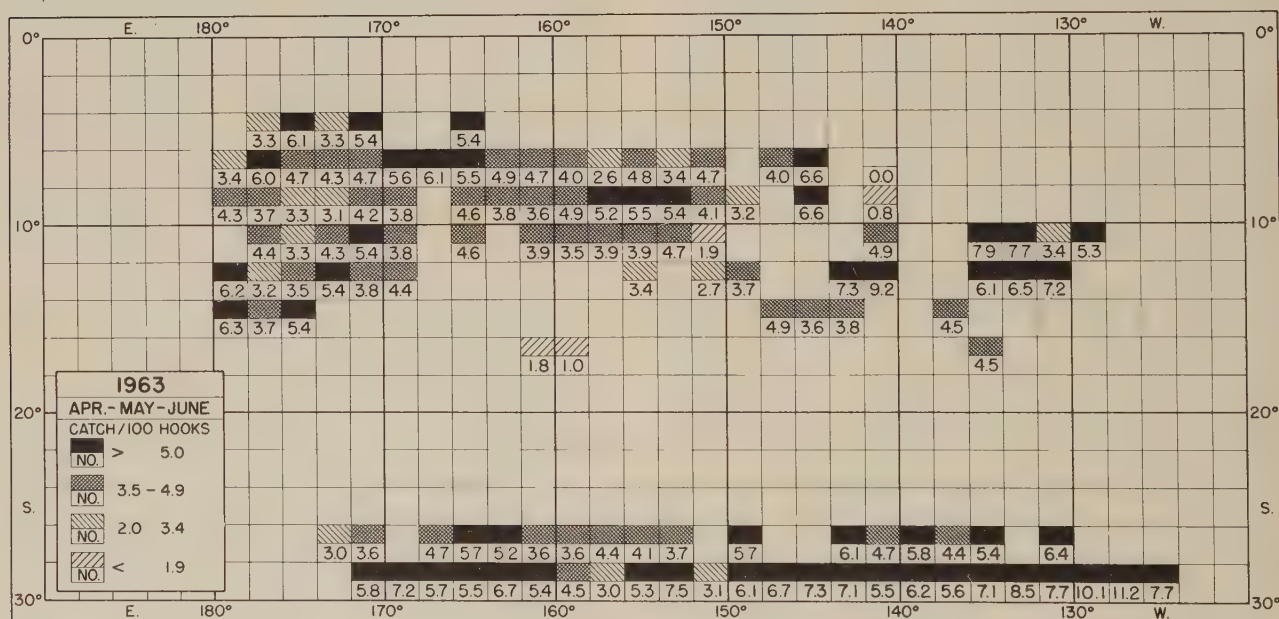
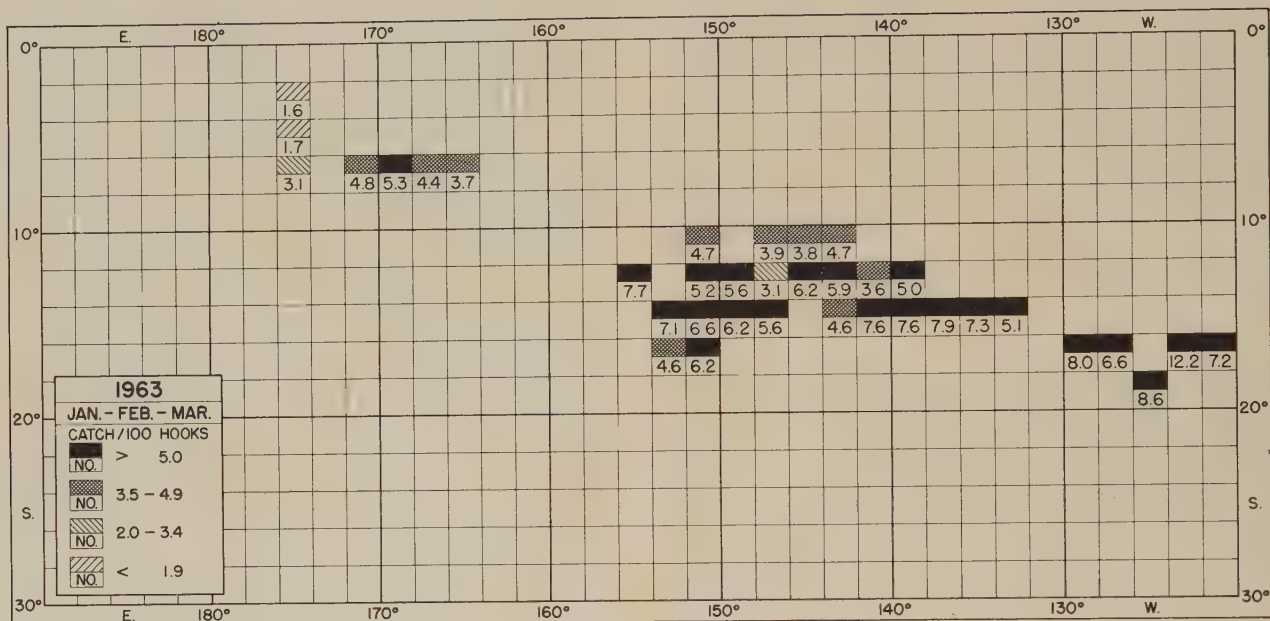
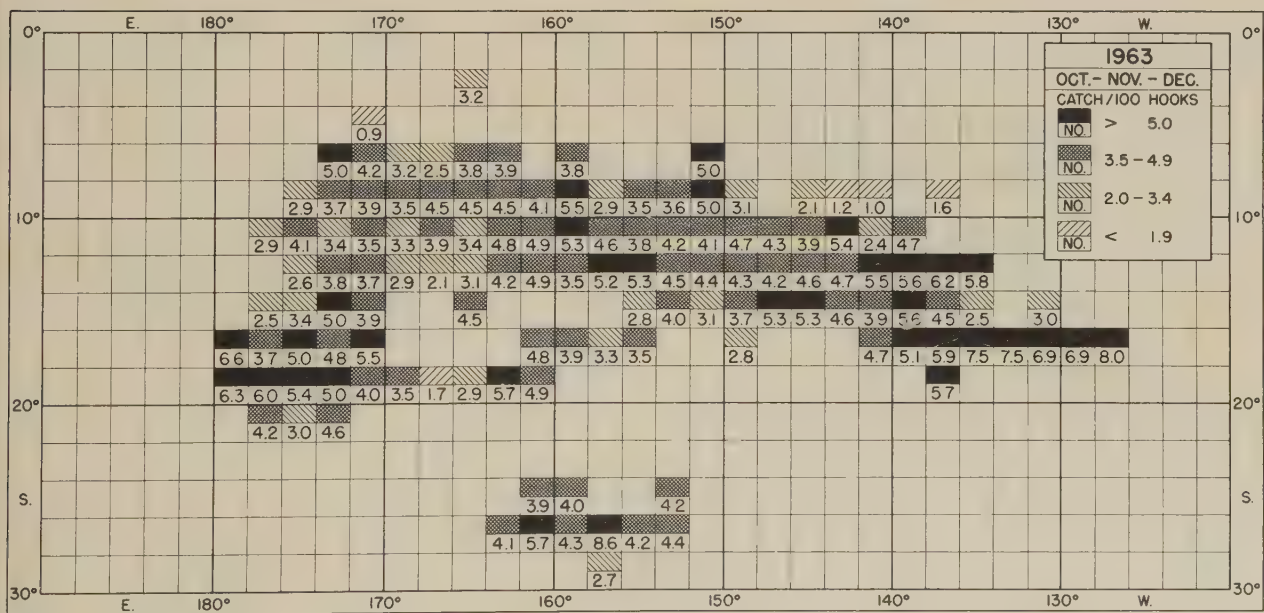
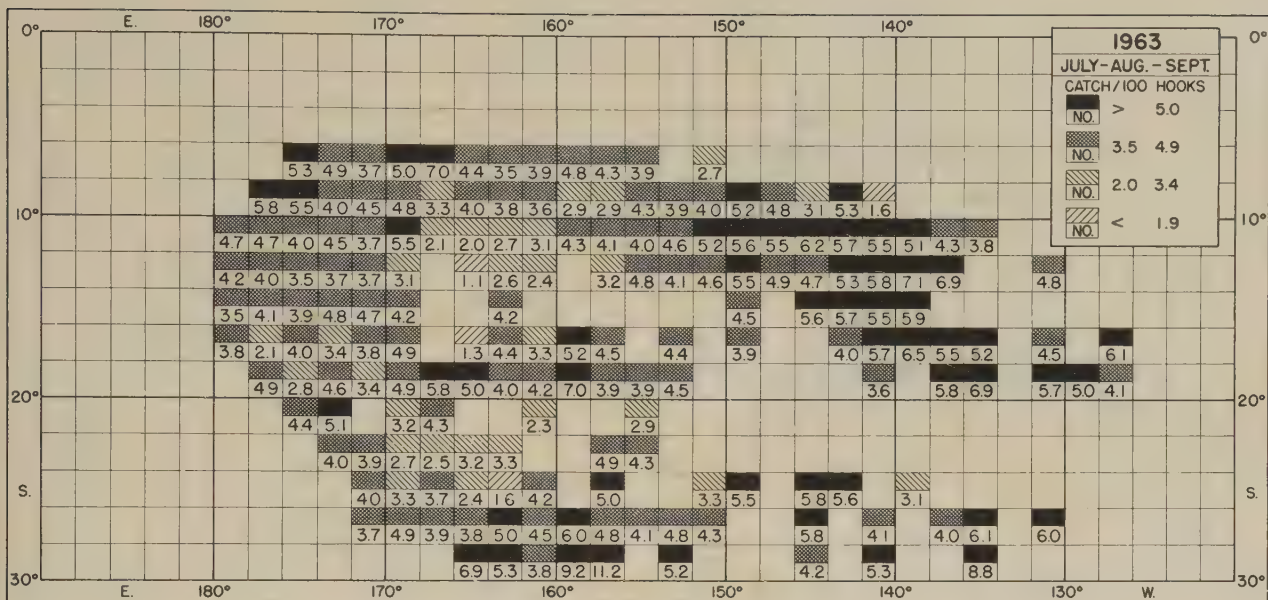


FIGURE 12.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1963.



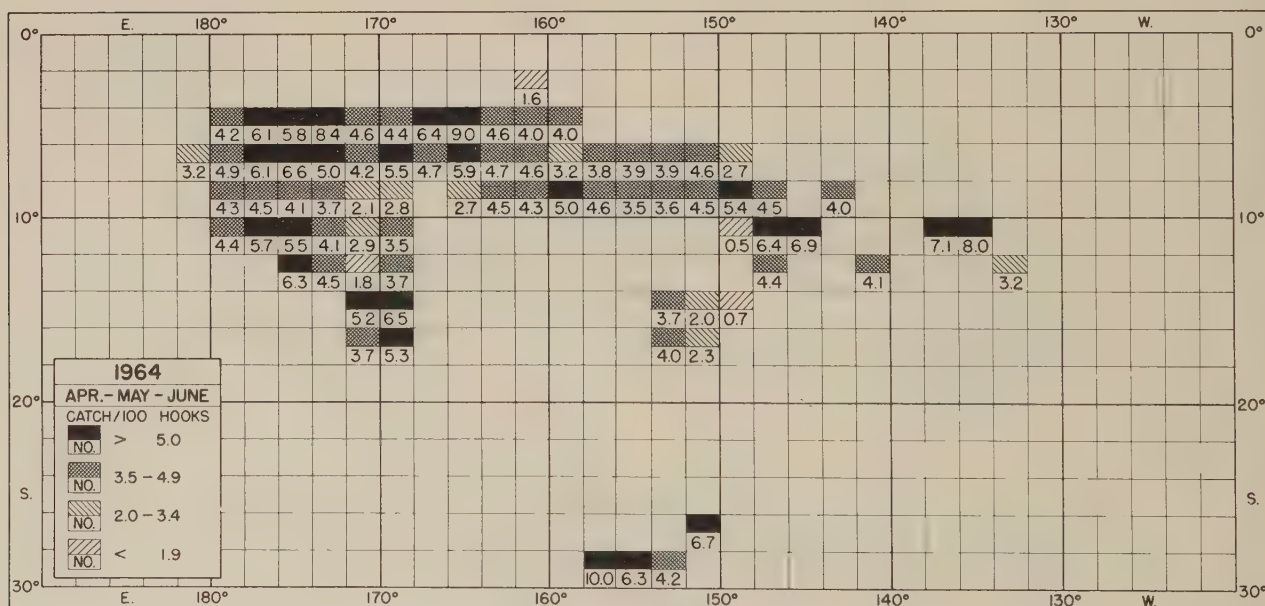
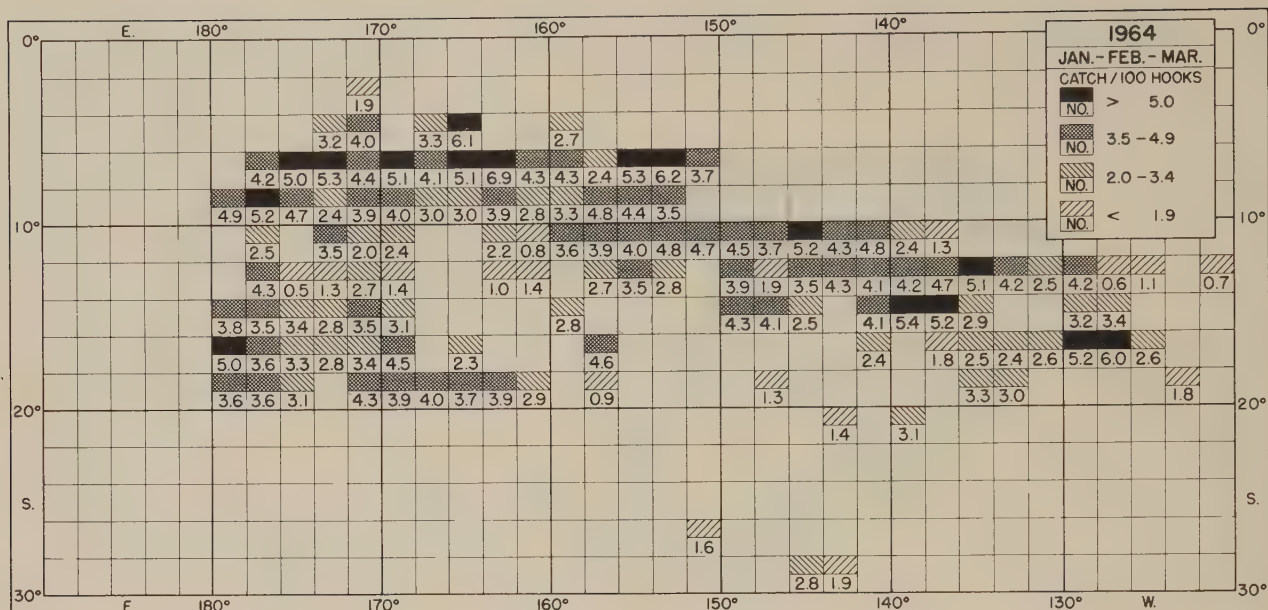
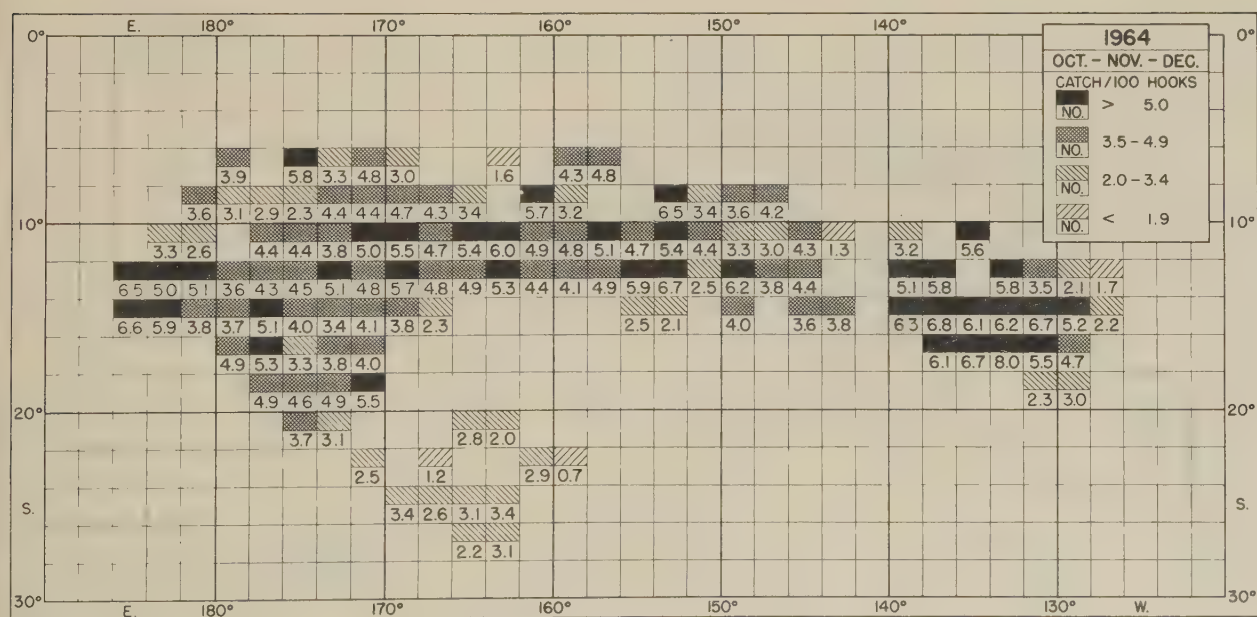
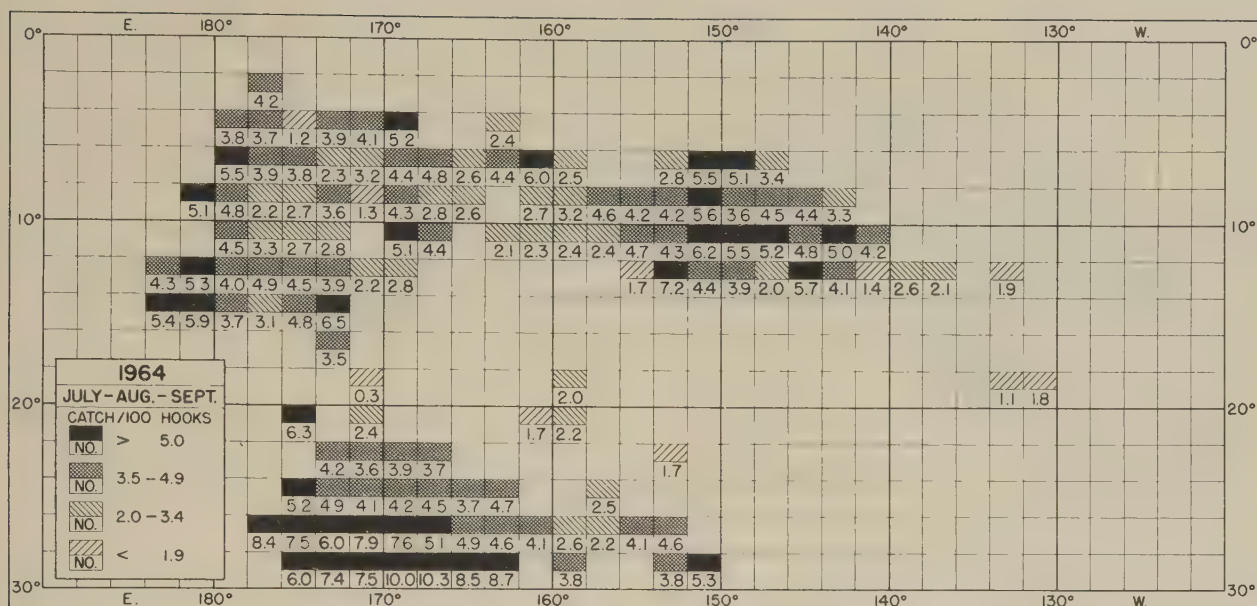


FIGURE 13.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1964.



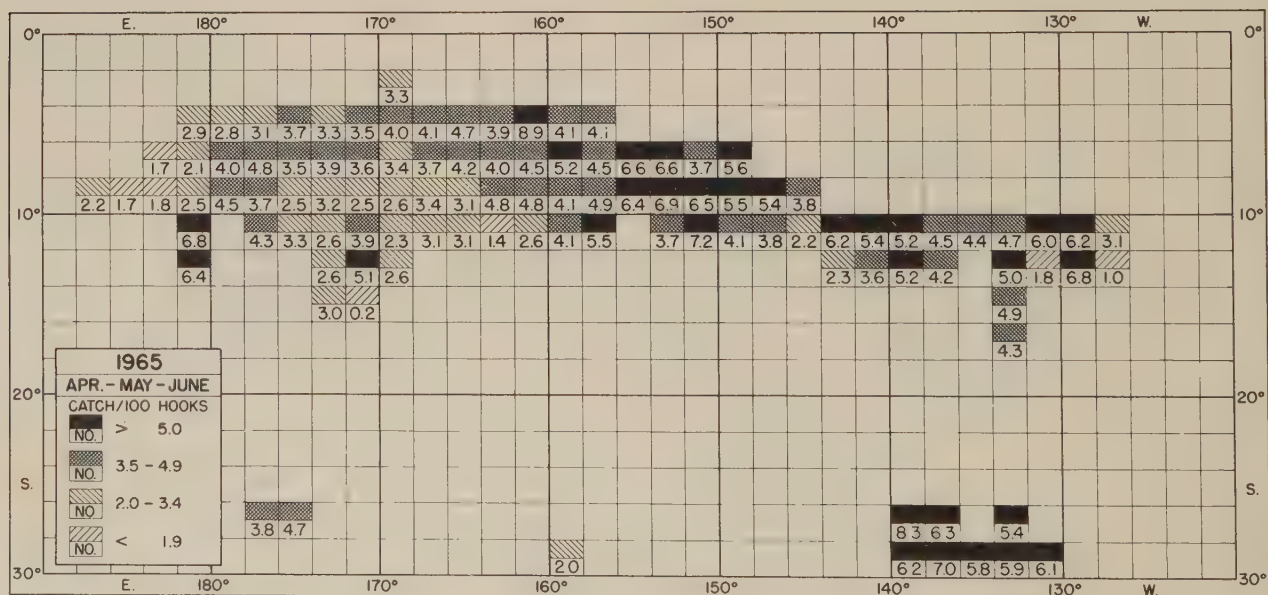
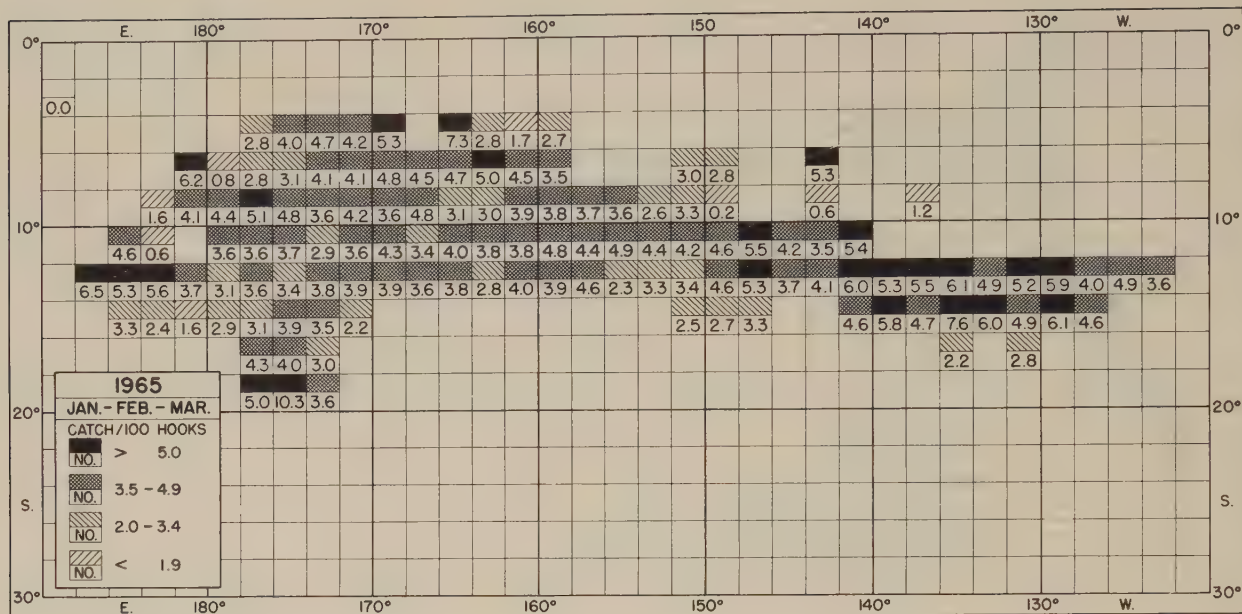
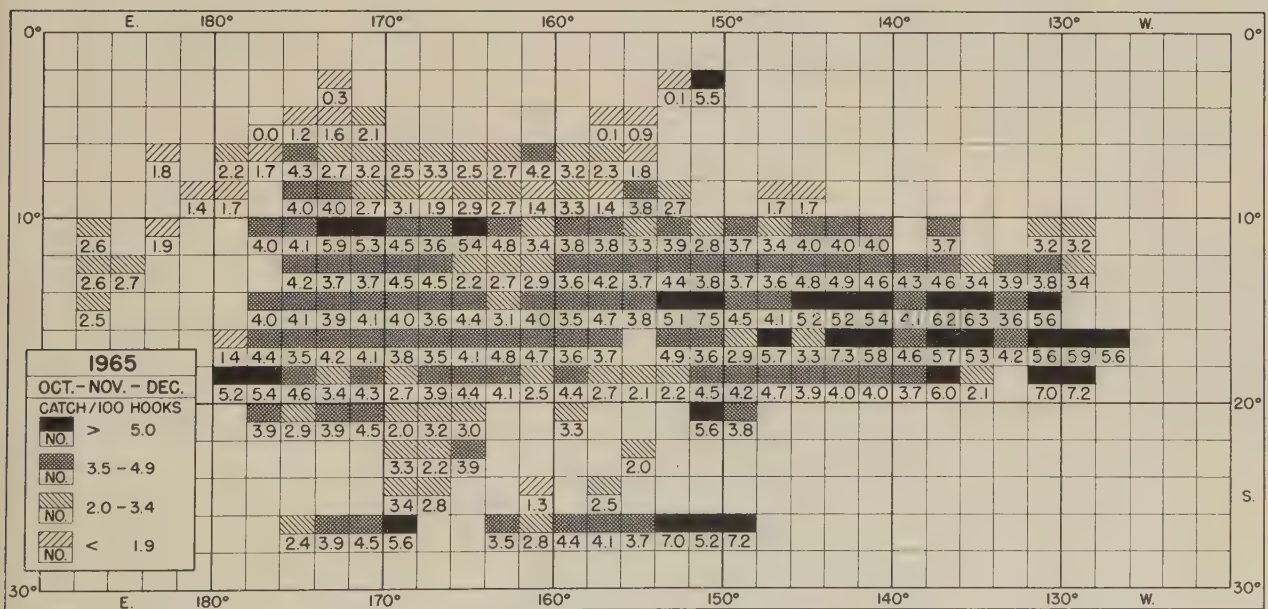
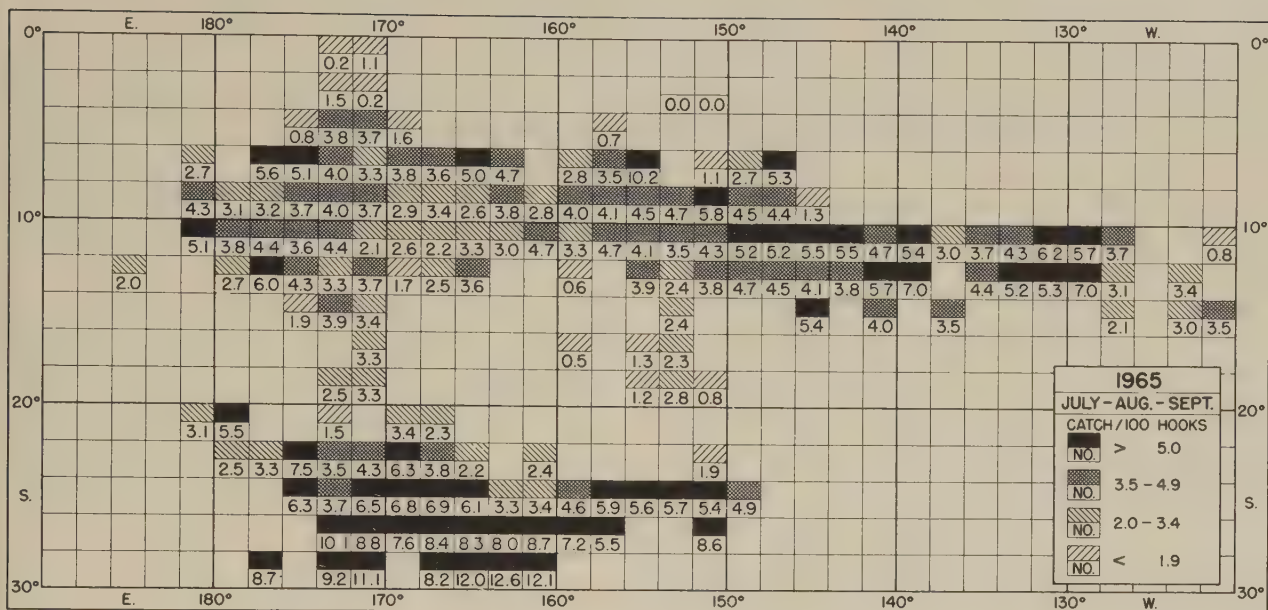


FIGURE 14.—The average catch rate (catch of albacore per 100 hooks) of American Samoa-based vessels shown by quarters of the year, 1965.



hooks) are scattered throughout the areas fished in all quarters of the year. A tabulation of the data by 5 degrees of latitude (table 3) indicates no

well-defined seasonal and geographical differences. Average catch rates declined slightly, however, in 1965 as compared with 1963.

TABLE 3.—Quarterly mean catch rates (number of fish per 100 hooks) of albacore and (in parentheses) the fishing effort (number of hooks) in the central and eastern South Pacific Ocean (long. 170° E. to 120° W.)

[From data of American Samoa-based vessels]

Item	Latitudes (S.), west of long. 150° W.								Latitudes (S.), east of long. 150° W.							
	0°-5°	6°-10°	11°-15°	16°-20°	21°-25°	26°-30°	31°-35°	Mean	5°-10°	11°-15°	16°-20°	21°-25°	26°-30°	31°-35°	Mean	
1963:																
Jan.-Mar.	3.5 (22,456)		6.0 (14,390)	5.4 (2,600)				5.0		5.8 (85,455)	7.6 (31,260)					6.7
Apr.-June		5.0 (1,019,395)	3.8 (151,765)	1.4 (3,080)		4.9 (263,370)	5.9 (9,000)	4.2	3.5 (22,786)	6.3 (86,780)	4.3 (7,935)		7.9 (295,362)			5.5
July-Sept.		4.3 (758,552)	4.4 (766,280)	4.4 (280,592)	4.1 (103,045)	5.2 (212,192)		4.5	5.2 (48,836)	5.7 (909,246)	4.1 (195,783)	5.5 (15,575)	5.2 (30,140)			5.1
Oct.-Dec.	1.1 (8,750)	4.3 (581,867)	4.5 (838,114)	4.4 (363,583)	4.4 (19,420)	4.4 (89,752)		3.9	1.7 (22,385)	5.2 (670,923)	5.7 (230,335)					4.2
Mean	2.3	4.5	4.7	3.9	4.3	4.8	5.9		3.5	5.8	5.4	5.5	6.6			
1964:																
Jan.-Mar.	1.5 (8,268)	4.4 (862,704)	3.4 (253,000)	3.3 (285,409)		1.6 (1,338)		2.8		4.3 (306,511)	4.1 (109,120)	.6 (3,838)	2.4 (4,296)	1.0 (6,000)		2.5
Apr.-June	2.3 (6,100)	5.0 (1,902,756)	4.6 (97,870)	4.7 (27,030)		7.0 (12,650)		4.7	4.6 (78,958)	4.6 (63,780)						4.6
July-Sept.	3.4 (15,158)	4.2 (347,279)	4.2 (299,406)	1.9 (3,830)	3.1 (111,030)	6.7 (536,836)		4.0	4.1 (73,908)	4.8 (164,804)	1.3 (9,120)					3.4
Oct.-Dec.		4.4 (167,910)	4.9 (1,706,235)	5.3 (141,804)	2.9 (47,896)	3.1 (20,172)		4.1	3.6 (43,866)	4.4 (191,028)	5.6 (279,708)					4.5
Mean	2.4	4.5	4.3	3.8	3.0	4.6			4.1	4.5	3.7	.6	2.4	1.0		
1965:																
Jan.-Mar.	3.9 (296,751)	4.2 (1,421,053)	3.8 (568,327)	4.2 (74,584)				4.0	2.0 (3,120)	5.0 (836,168)	2.4 (24,930)					3.1
Apr.-June	2.6 (74,692)	4.3 (2,708,555)	4.7 (137,720)			3.1 (6,420)	1.7 (1,620)	3.3	5.5 (124,124)	5.6 (242,129)	4.3 (3,120)		6.6 (172,690)	7.7 (13,836)		5.9
July-Sept.	2.7 (63,400)	4.0 (970,613)	3.8 (447,249)	2.6 (38,976)	4.5 (249,438)	8.0 (739,899)		4.3	3.3 (109,834)	4.8 (566,903)	2.0 (5,894)	4.9 (5,170)	5.0 (3,600)			4.0
Oct.-Dec.	2 (22,420)	3.0 (380,594)	4.1 (910,555)	4.0 (1,327,684)	3.7 (100,038)	3.7 (111,977)		3.1	1.7 (1,458)	5.4 (699,574)	4.7 (518,535)	3.8 (2,700)	7.2 (11,230)			4.6
Mean	2.4	3.9	4.1	3.6	4.1	4.9	1.7		3.1	5.2	3.4	4.4	6.3	7.7		

To gage the abundance of albacore in areas not fished by the American Samoa-based vessels, some Japanese data were tabulated (table 4). Data for 1958-63 indicate that albacore are not as abundant in the western South Pacific Ocean, between long. 140° E. and 180°, as in areas fished by vessels from American Samoa. The catch rates, averaging less than two albacore per 100 hooks, are lower than those in more eastern waters. Perhaps some of the difference may be due to the selective fishing for albacore by American Samoa-based vessels, whereas in more western areas, the vessels from Japan may be fishing primarily for other species. Subtle differences in the fishing gear, such as in the lengths of the various lines, are known to affect the catch rates of albacore. It is probable, however,

that these catch rates reflect the actual abundance of albacore in these areas.

Seasonally, the best catch rates in the western South Pacific are obtained in May through September. Latitudinally, the mean catch rates increase southward from the Equator, and the best catches are generally made between lat. 15° and 30° S. Koto (1966) found the best catch rates in the South Pacific during 1950-61 between lat. 10° and 30° S. and reported peaks of abundance along lat. 20° S. The catch rates south of lat. 30° S. were lower. In the areas fished by the American Samoa fleet, the catch rates are also low near the Equator but do not change as markedly from north to south. Generally, catch rates are also higher in the southernmost areas fished, between lat. 25° and 30° S.

TABLE 4.—Pooled monthly mean catch rates of albacore (catch per 100 hooks) in the western South Pacific Ocean (long. 140° E. to 180°), 1958-63

[From data provided by the Nankai Regional Fisheries Research Laboratory, Kochi, Japan, and those published by the Japan Fisheries Agency (1965, 1966)]

S. latitude	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
0°-5°	<0.1	0.1	1.2	0.2	0.2	0.3	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	0.7
6°-10°	.3	.4	.5	.6	.8	1.7	1.5	1.3	.7	.5	.4	.2	.9
11°-15°	1.7	1.6	1.5	2.3	2.1	2.5	2.9	2.4	2.2	1.6	1.3	1.0	1.3
16°-20°	2.3	1.3	1.1	2.5	3.0	2.2	2.8	3.0	2.7	2.7	1.9	2.2	2.9
21°-25°	1.0	.8	.0	1.1	1.3	3.8	4.2	4.1	2.8	1.6	1.2	1.4	1.3
26°-30°	.2		.0	1.0	3.5	4.5	4.6	4.0	3.1	1.9	1.2	.8	2.3
31°-35°	1.4			1.6	2.7	3.8	.9	.8	.9	1.2	2.3	2.6	1.8
36°-40°	.6				1.3	1.2	.8	.6	.7	.8	1.1	2.3	1.0
41°-45°			.3	1.2	1.2	.8	.7			.2	1.2	1.6	.9
46°-50°				.6	.2	.2							.3
Mean	.9	.8	.7	1.2	1.6	2.1	2.1	2.0	1.6	1.2	1.2	1.3	

In general, the distribution of albacore is continuous from west to east, at least between long. 140° E. and 120° W. in the South Pacific Ocean. A difference between the eastern and western South Pacific Ocean is in the apparent abundance of albacore; catch rates are lower in the western South Pacific Ocean.

SIZE OF ALBACORE

The albacore taken by the American Samoa-based fishery generally range from about 70 to 110 cm. long; 95 percent of the fish fall between 80 and 105 cm. (fig. 15). Among fish longer than

90 cm., males greatly outnumber females. The average length of albacore in 1965 was 88 cm. for females and 93 cm. for males.

CHANGES IN SIZE OF ALBACORE

In 2 of the 3 years during which length data were obtained, the mean length of fish declined sharply during February-April (fig. 16). This decrease could have resulted from shifts in fishing grounds, seasonal variation in fish sizes on the fishing grounds, or both. The trend toward a decrease in length from February 1964 to August 1965 may have been caused by the entry into the

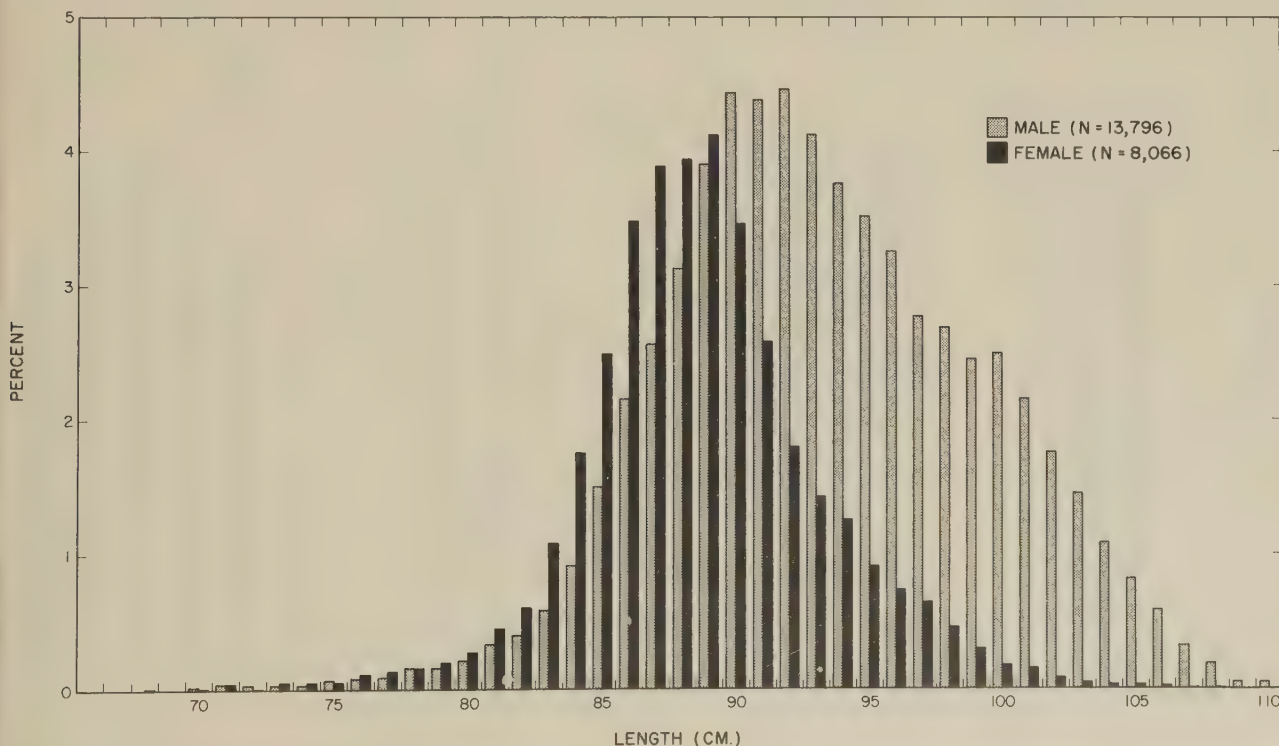


FIGURE 15.—Composite length-frequency distribution of albacore landed by the American Samoa-based longline vessels during 1965.

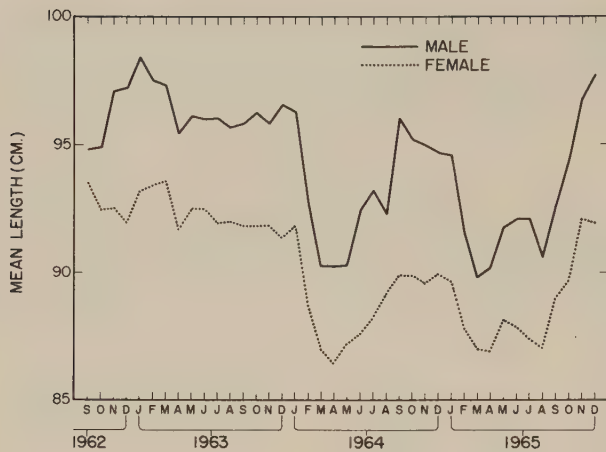


FIGURE 16.—Monthly mean lengths of albacore landed at American Samoa, September 1962 to December 1965.

fishery of an abundant year class or by a general decrease in the abundance of the older, larger fish in the stock. To determine if either of these factors might contribute to the decrease in mean length

during February–April, we shall examine the size data in more detail.

DIFFERENCES IN FISH SIZE BY LATITUDE AND LONGITUDE

The mean length of albacore taken within 5-degree latitudinal bands (fig. 17) tends to increase from north to south. The fish are smallest near the Equator and largest at lat. 20° to 25° S. Albacore tend to be small again south of 25° S. These results are in general agreement with the findings of Honma and Kamimura (1957), although in contrast to these workers, we did not observe any significant increase in the size of albacore to the north of lat. 10° S. with the exception of 1963.

No longitudinal trend is noticeable. Honma and Kamimura found a general tendency for the size of albacore to increase from west to east. These authors, however, examined data from the western South Pacific between long. 140° E. and 170° W.,

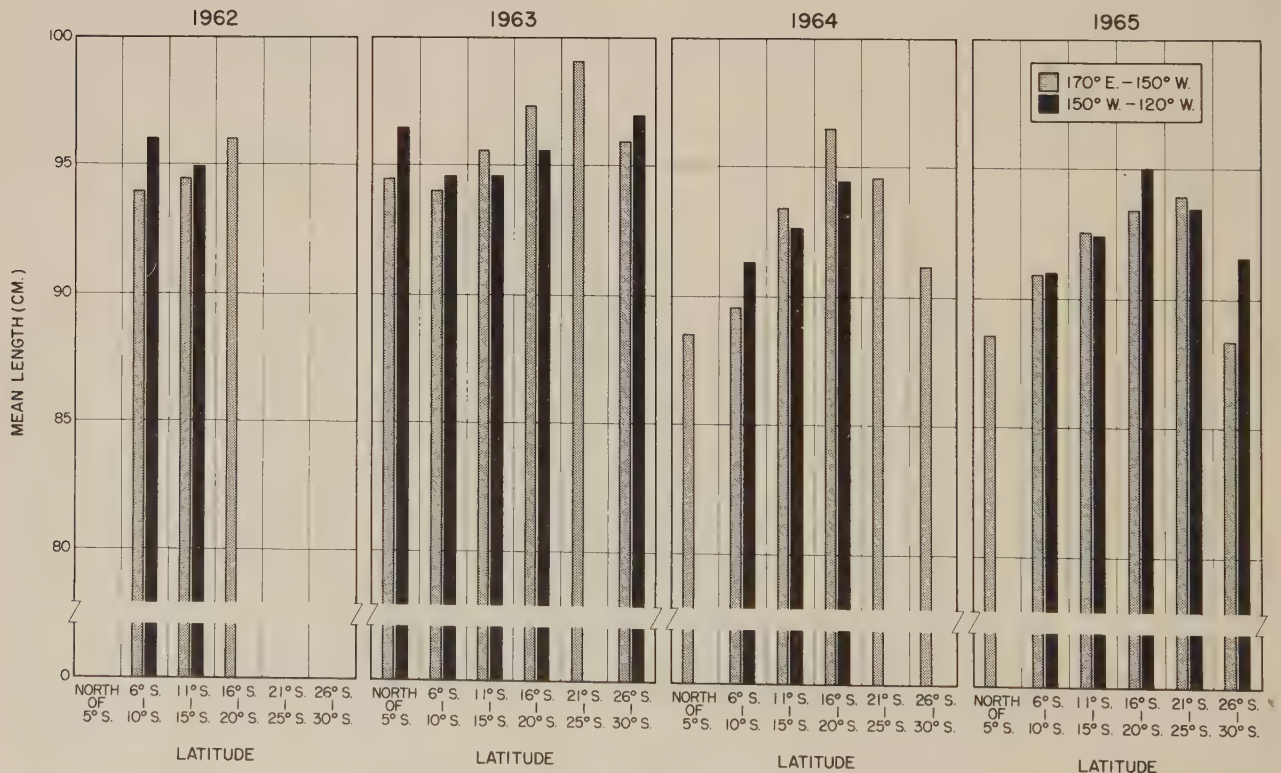


FIGURE 17.—Annual mean lengths of albacore (sexes combined) taken by the American Samoa-based vessels, by latitudes, 1962–65.

whereas our data cover a different segment of the ocean, from long. 170° E. to 120° W.

SIZE CHANGES DUE TO SHIFTS IN FISHING GROUNDS

Since average fish size is known for each area, it is possible to determine to what extent selection of fishing ground is responsible for changes in fish sizes in the landings. The shifting of the fishing effort from one area to another is readily seen (table 5). The regular shift of fishing grounds in 1964 and 1965 accounted for a large measure of the size changes in the landings. The average size of albacore decreased in March and April of both years when nearly all of the catches came from the

area north of lat. 10° S. where the fish are smaller. For example, when the average size first began to decrease in February 1964, 68.7 percent of the catch was made between 6° and 10° S., where the albacore are small. During March, April, and May, when the average sizes were smallest of the entire year, 84.8, 93.5, and 93.0 percent, respectively, of the landings came from this area. The sizes gradually increased as fishing shifted to other areas. The same situation was repeated in 1965. In contrast, fishing was less concentrated in these northernmost waters during the early months of 1963. In March, April, and May, for example, only 20.0, 73.0, and 70.3 percent, respectively, of the landings came from lat. 6° to 10° S.

TABLE 5.—The monthly mean length of albacore, and (in parentheses) the estimated percentage of the total catch from each locality by American Samoa-based vessels, shown by 5 degrees of latitude in the central South Pacific

Item	Latitudes (S.), west of long. 150° W.						Latitudes (S.), east of long. 150° W.					
	North of 5°	6°-10°	11°-15°	16°-20°	21°-25°	26°-30°	North of 5°	6°-10°	11°-15°	16°-20°	21°-25°	26°-30°
1963:												
January.....		96.1 (10.7)	95.9 (38.4)	95.8 (14.3)					95.8 (25.0)	94.7 (8.3)	92.1 (1.5)	93.0 (1.7)
February.....		96.5 (25.0)	95.9 (32.1)	96.4 (25.0)					96.7 (17.9)			
March.....	96.0 (5.0)	96.8 (20.0)	96.3 (20.0)	96.3 (25.0)			96.4 (5.0)	95.0 (10.0)		96.4 (15.0)		
April.....	92.9 (2.5)	93.8 (73.0)	95.2 (2.5)					94.9 (14.3)	94.4 (5.1)			100.1 (2.5)
May.....		94.0 (70.5)	95.3 (3.1)					94.5 (2.0)	94.5 (3.1)			97.8 (21.5)
June.....		93.4 (40.7)	95.5 (14.9)			96.4 (20.2)		92.3 (4.0)				95.4 (2.2)
July.....		93.6 (50.0)	96.5 (3.6)	99.7 (10.7)					94.9 (21.4)	97.1 (10.7)		94.8 (3.6)
August.....		93.7 (19.5)	95.8 (34.1)	100.2 (2.4)	98.9 (2.4)	96.0 (2.4)		94.2 (2.4)	94.2 (29.2)	95.4 (7.3)		
September.....		94.5 (31.0)	94.2 (6.9)	98.5 (10.3)	97.8 (6.9)	95.6 (3.4)		94.4 (3.4)	93.8 (37.9)			
October.....		94.9 (19.3)	95.1 (19.3)	96.8 (9.7)	101.8 (3.2)	94.6 (6.5)		95.1 (6.5)	94.5 (32.3)	96.2 (3.2)		
November.....		93.2 (31.5)	95.7 (19.6)	98.0 (4.6)					96.4 (31.7)	94.7 (12.5)		
December.....		92.6 (35.4)	92.9 (5.6)	97.7 (30.9)					93.9 (8.4)	95.0 (19.6)		
1964:												
January.....		92.5 (22.4)	94.9 (14.5)	96.8 (42.7)					93.8 (20.4)			
February.....		90.3 (68.7)	94.9 (3.5)	96.5 (10.4)					92.9 (17.4)			
March.....	89.2 (6.1)	88.7 (54.8)						87.8 (3.0)	92.5 (3.0)	95.2 (3.0)		
April.....		88.9 (93.5)	94.1 (3.2)						88.9 (3.2)			
May.....		88.7 (93.0)				90.6 (3.5)		90.0 (3.5)				
June.....	87.8 (3.3)	90.2 (70.0)	90.4 (3.3)	95.5 (3.3)				91.5 (10.0)	91.2 (10.0)			
July.....		90.7 (35.7)	96.0 (19.5)	97.7 (1.9)		87.9 (23.4)		91.9 (11.7)	92.3 (7.8)			
August.....		89.6 (27.6)	94.2 (13.8)		89.3 (6.9)	91.0 (34.5)		92.3 (13.8)	93.6 (3.4)			
September.....		91.8 (5.1)	95.2 (30.8)		95.1 (28.2)	94.4 (25.6)		92.9 (5.1)	91.3 (5.1)			
October.....		92.2 (15.4)	92.9 (57.7)	98.2 (3.8)	97.0 (3.8)	95.8 (3.8)		91.0 (3.8)	91.0 (3.8)	93.7 (7.7)		
November.....		91.0 (9.9)	92.6 (71.6)	95.4 (8.6)					94.0 (3.3)	95.1 (6.6)		
December.....		90.7 (7.6)	92.9 (73.5)	95.0 (7.6)					93.9 (7.6)	93.5 (3.8)		
1965:												
January.....		91.1 (16.8)	94.3 (23.5)	93.1 (16.8)				92.1 (2.8)	93.2 (40.1)			
February.....		89.6 (63.3)	87.4 (3.3)					90.0 (3.3)	92.1 (30.0)			
March.....		87.7 (88.9)							92.1 (11.1)			

TABLE 5.—The monthly mean length of albacore, and (in parentheses) the estimated percentage of the total catch from each locality by American Samoa-based vessels, shown by 5 degrees of latitude in the central South Pacific—Continued

Item	Latitudes (S.), west of long. 150° W.						Latitudes (S.), east of long. 150° W.					
	North of 5°	6°-10°	11°-15°	16°-20°	21°-25°	26°-30°	North of 5°	6°-10°	11°-15°	16°-20°	21°-25°	26°-30°
1965—Continued												
April.....	87.6 (22.0)	88.9 (78.0)										
May.....	89.8 (8.0)	89.9 (60.0)	91.7 (4.0)					90.5 (24.0)				92.9 (4.0)
June.....		90.0 (60.5)	94.6 (4.9)			88.4 (7.4)		91.2 (4.9)	90.8 (17.3)			90.2 (4.9)
July.....	89.0 (3.1)	91.2 (37.5)	97.2 (6.3)	83.6 (3.1)		84.5 (15.6)		91.4 (18.7)	91.3 (15.6)			
August.....	87.1 (3.0)	90.0 (33.3)	87.3 (6.1)	90.3 (3.0)	89.5 (21.2)	85.8 (18.2)			91.9 (15.2)			
September.....	89.5 (6.8)	89.9 (13.7)	93.3 (11.0)	94.7 (2.0)	91.5 (33.3)	89.6 (13.7)		90.6 (2.0)	91.2 (9.8)	90.4 (3.9)	92.4 (3.9)	
October.....		91.0 (40.5)	91.5 (13.5)	97.6 (13.5)	96.7 (8.1)	89.0 (2.7)			92.5 (18.9)			
November.....		93.3 (11.4)	94.5 (25.0)	97.1 (38.6)	98.0 (2.3)	92.6 (2.3)			93.8 (18.1)	98.1 (2.3)		
December.....		97.9 (2.1)	94.0 (25.0)	97.5 (43.7)					94.6 (10.4)	96.5 (18.8)		

In spite of the widespread knowledge among fishermen that fish are smaller in the more northern waters (north of lat. 15° S.), they persist in fishing these waters during February–May because of their belief that the higher catch rates will more than compensate for the smaller sizes of fish. Fishing effort was concentrated in these waters during the early months of both 1964 and 1965. This type of selection has undoubtedly contributed to the general size decrease of albacore in the landings in those two years.

SEASONAL VARIATION IN FISH SIZES

Although we can generalize that sizes of albacore change with latitude, seasonal variation in sizes within the same areas is also considerable. For example, the average sizes of albacore taken from the area between lat. 6° and 10° S. were smallest during February–May in both 1964 and 1965, as compared with the rest of the year (fig. 18). The decrease in size may be explainable to a large extent by the fact that the vessels concentrate their fishing north of 10° S. where the fish are smaller; this effect on fish size is further aggravated by the coincidental presence of smaller fish in the area at that particular time of the year.

DECREASE OF OLDER FISH IN STOCK

Albacore taken in 1964 and 1965 were shorter on the average than those caught in 1963 and perhaps earlier (figs. 16 and 17 and table 5). This decrease in size may be attributable, at least in part, to an actual decrease of older, larger fish in the stock. A decrease of this magnitude might be expected

when a stock undergoes exploitation, because increasing fishing mortality over the years increases total mortality. As total mortality increases, the average age and, thus, the average size of the stock must decline.

EFFECT OF ABUNDANT YEAR CLASS ON SIZE COMPOSITION

Numbers of larger fish of both sexes decreased from September 1962 to about May 1965, while smaller fish (<90 cm.) tended to increase (figs. 19 and 20). Superimposed on this general increase of smaller fish was an abrupt, exceedingly large increase beginning around February 1964. This rise of apparent abundance of smaller fish suggests the possibility of the entry into the fishery of an abun-

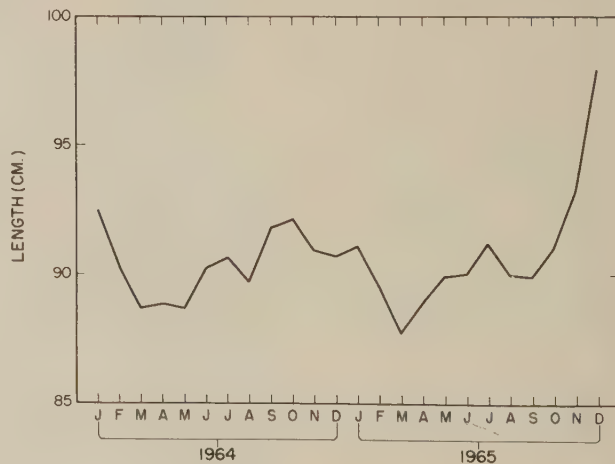


FIGURE 18.—The monthly mean length of albacore (sexes combined) taken by American Samoa-based vessels in the area 6° to 10° S., 170° E. to 150° W., in 1964 and 1965.

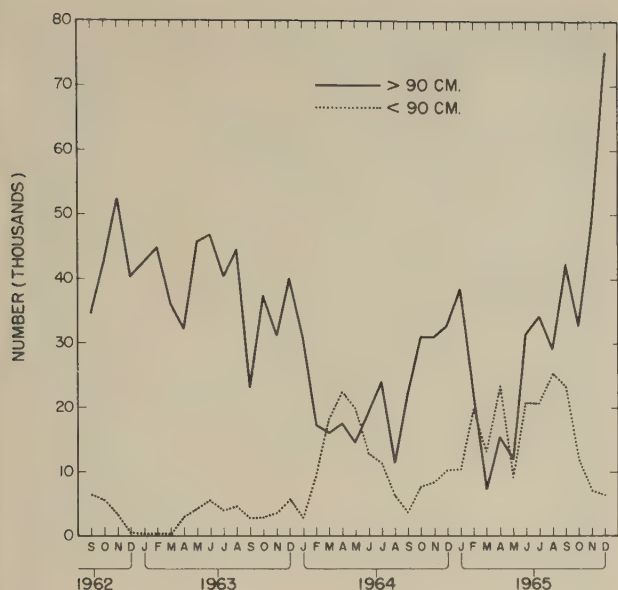


FIGURE 19.—Estimated numbers of two size categories of male albacore landed by the American Samoa-based fishery, September 1962 to December 1965.

dant year class. If so, we would expect that the numbers of larger fish—those longer than 90 cm.—would increase as this large year class moved through the fishery. Such an increase is indicated by the data. The abrupt increase in small fish in February 1964 was followed by an increase in larger fish toward the latter part of 1964. Near the end of 1964 and in early 1965, an increase in the number of small fish of both sexes was followed by an increase in longer fish a few months later.

A large part of this change in size composition is attributable to shifts of fishing grounds, as discussed previously. Year-class strength, however, is

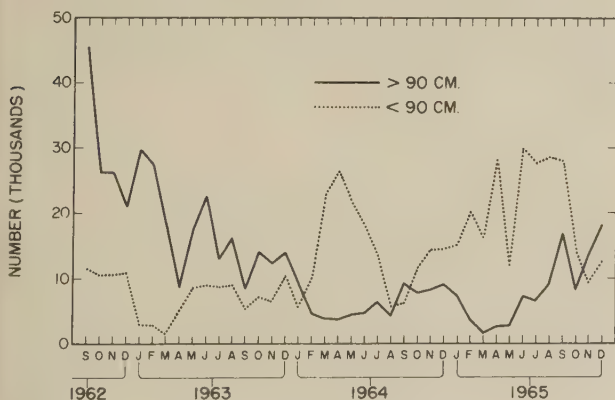


FIGURE 20.—Estimated numbers of two size categories of female albacore landed by the American Samoa-based fishery, September 1962 to December 1965.

probably also an important contributor to the apparent changeover in size composition during the 3-year period. Analysis of data from a few more years would clarify this question.

SEX RATIO OF ALBACORE

Changes in sex ratio could also affect the size composition of the landings since the monthly mean lengths of male albacore are from 1 to 6 cm. greater than those of females.

The proportion of males in the total landings (fig. 21) has fluctuated greatly without noticeable trend over the years. On the other hand, the proportion of males among the larger fish (>90 cm.) increased through September 1964, after which it tended to level out.

Although males averaged around 62 percent of the monthly landings between September 1962 and December 1965, their percentage did decrease in 1964 and 1965 during periods corresponding to months of reduced mean sizes (i.e., February–June 1964, February–August 1965). Though the mean lengths of both sexes decreased simultaneously during these months (fig. 16), the coincidental re-

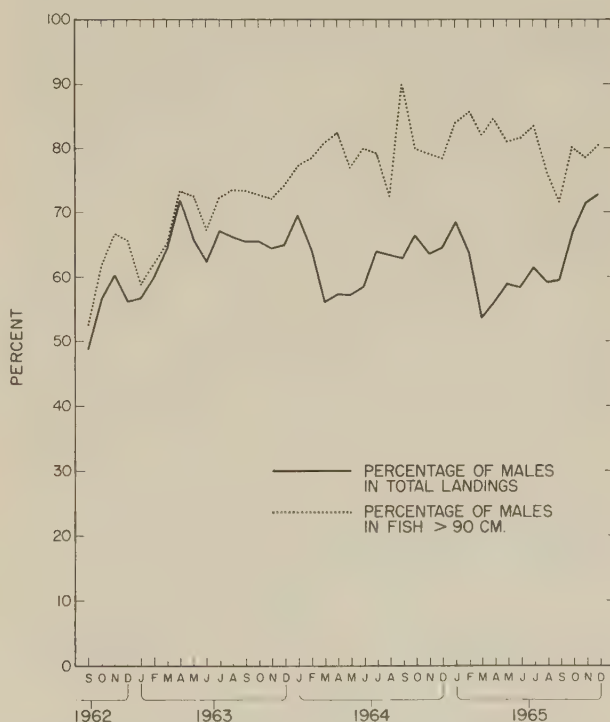


FIGURE 21.—Monthly sex ratio of albacore landed by the American Samoa-based vessels.

duction in the proportion of males has acted to amplify the general size decrease. This influence was reflected in the decreased catch per 100 hooks (by weight) during these months (fig. 9).

SUMMARY

1. This report is based on (a) data on landings provided by the two tuna packing firms operating in American Samoa, (b) catch and effort data provided by the operators of American Samoa-based fishing vessels, (c) size and sex data on albacore sampled at the tuna canneries in American Samoa, and (d) Japanese data made available to us by the Japan Fisheries Agency.

2. The tuna fishery based in American Samoa began in 1954 with a fleet of seven Japanese longline vessels. The fleet grew rapidly and in 1965, 154 vessels fished out of American Samoa. The composition of the fishing fleet, in terms of country of origin of the vessels, has changed. In the early years of the fishery, the fleet was composed entirely of longliners from Japan. The 105-vessel fleet operating during the last quarter of 1965 was composed of 62 vessels from Japan, 30 from the Republic of Korea, and 13 from the Republic of China.

3. The fishery was confined to the immediate vicinity of the Samoa Islands in the early years, but has expanded rapidly to the east and south. In 1965, the fishery area was bounded on the north by the Equator, on the south by lat. 30° S., on the west by long. 175° E., and on the east by about long. 120° W. These boundaries enclose an area of about 23 million square kilometers.

4. Though a variety of pelagic fishes is taken by the longline fishery, albacore command the highest price at the canneries and are, for this reason, fished for selectively. Data provided by the fishermen are complete only with respect to the albacore catches, the major species taken. Consequently, no attempt was made in this report to analyze the data on the other tuna species.

5. The annual landings of albacore in American Samoa have gradually increased from 338 metric tons in 1954 to 15,588 metric tons in 1965.

6. The occurrence of albacore in the South Pacific Ocean exhibits no clear seasonality although in most years landings have been slightly better during the latter half of the year.

7. The catch of albacore per fishing trip was used as the measure of apparent abundance for

the entire period of the fishery's existence. No other unit of effort was available before 1959 when data first were recorded on number of days fished per trip and 1963 when we began to collect data on number of hooks fished per day. This index proved to be reasonably satisfactory, however, because neither the average number of days fished per trip nor the size composition of the vessels has varied appreciably over the years covered by our study.

8. The catch per trip (in terms of weight of fish) tends to increase with size of vessel, mainly because (1) larger vessels generally fish more gear than smaller vessels, and (2) their trips tend to be longer. However, the fact that relatively few vessels in the American Samoa fleet were larger than 120 tons or smaller than 80 tons permits the use of catch per trip as an index of apparent abundance.

9. The catch per trip tended to increase steadily through 1960, tapered off, and stabilized at a lower level in 1963 and 1964. There was again a slight increase in 1965.

10. Annual landings have tended to be directly proportional to the total amount of fishing effort.

11. The size of the vessel does not significantly affect the catch rate in terms of catch per 100 hooks fished.

12. The distribution of albacore is continuous from west to east in the South Pacific Ocean, at least between long. 140° E. and 90° W. The fish have their greatest abundance, however, in the central and eastern South Pacific Ocean between 180° and 120° W.

13. During the first half of the year, the American Samoa-based vessels generally fish north of lat. 20° S., where catches are most favorable. In later months, beginning about June or July, the albacore longline fishery moves southward to as far as lat. 30° S.

14. The number of albacore caught per 100 hooks did not vary appreciably in 1963-65. But owing to the decrease in average size of albacore caught, the weight of fish landed per 100 hooks declined significantly in 1964 and early 1965.

15. The mean lengths of albacore landed in American Samoa did not change significantly from September 1962 to January 1964, but suddenly became smaller in February 1964. Although the mean length increased slightly after May, the fish remained smaller than in 1962-63. The average

length again decreased in February 1965, but by the end of the year the albacore landed in Samoa were even larger than in 1962-63.

16. Several factors are responsible for changes in mean lengths of albacore. One of the primary causes is change of fishing grounds; fishing is confined during the early months of the year to more northern waters, north of lat. 15° S., where the albacore tend to be small. As some of the fishing shifts southward beginning about June or July, the lengths of albacore gradually increase since the largest fish occur near lat. 20°-25° S. Albacore are smaller to the south of lat. 25° S.

17. We found no longitudinal differences in average fish sizes.

18. The general decrease in average lengths of albacore taken in 1964 as compared to 1962-63, may have been due in part to an abundant year class of small albacore that entered the fishery early in 1964. As this year class moved through the fishery, average size increased slightly toward the latter part of 1964. The data suggest that another large year class of small albacore entered the fishery early in 1965.

19. Although albacore are generally smallest in areas north of 15° S., sizes also vary seasonally within the same areas. The fish are smallest during February-May when coincidentally the vessels tend to concentrate their fishing in this northern area.

20. Males average 1 to 6 cm. longer than females each month; therefore, any change in the sex ratio affects the average size of fish in the catch. Indeed, during the periods of reduced mean sizes in 1964 and 1965, the percentage of males decreased, permitting the smaller females to have an unusually depressing effect on the average size of the albacore. The smaller catch (in weight) per unit of effort could be attributed partly to the change in sex ratio.

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ued success of the field station in providing data from the fishery is due to the cooperation of the management and staff of the Van Camp Sea Food Company-Samoa and the recently established (1963) Star-Kist Samoa, Inc., who allow our personnel to sample the landings at their canneries. The fishing vessel operators from Japan, the Republic of Korea, and the Republic of China provided us with detailed information on their fishing operations.

The fishery technicians from the BCF Laboratory in Honolulu who have served and continue to serve at the field station have collected the data used in this study. Andrew Scanlan of Samoa assisted our personnel at the field station.

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MICRONEKTON OF THE EASTERN TROPICAL PACIFIC OCEAN: FAMILY COMPOSITION, DISTRIBUTION, ABUNDANCE, AND RELATIONS TO TUNA^{1 2}

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ABSTRACT

The taxonomic composition and distribution of micronekton (fishes, crustaceans, and cephalopods about 1 to 10 cm. in largest dimension) were studied from catches of night net hauls in the upper 90 m. in most parts of the eastern tropical Pacific Ocean. One type of haul (net 1.5 m. square at mouth, uniform mesh size throughout, hauled obliquely at ship speed of 5 knots) contributed most of the data and is considered to be superior to any other existing type of haul with a net or trawl of comparable size for quantitative work on micronekton.

Ten families (Myctophidae, Gonostomatidae, Galatheididae, Euphausiidae, Penaeidae, Squillidae, Portunidae, Sergestidae, Enoploteuthidae, and Cranchiidae) and one suborder (Apodes: leptocephali) contributed 93.4 percent of the volume of the total catch. Some of these groups are localized, and others are widely distributed geographically; abundance varies according to the distribution of physical phenomena

which are responsible for eutrophic conditions. Agreement in family composition was poor for fishes between the net catches and the stomach contents of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Euthynnus pelamis*) from the same areas; agreement between catches and stomach samples was fair for crustaceans. The reasons for the differences are discussed. The commonly held opinion, that tunas are opportunistic feeders, within their sensory limitations, remains tenable.

To the extent that the net hauls sample kinds of micronekton which are important as food for tunas, they can be used to compare quantities of tuna prey in different areas. This comparison shows that the richest tuna forage is off western Baja California and that an area west of Ecuador and northern Peru with practically no surface fishing probably has about as much forage as some areas which support commercial surface fishing.

Comprehensive biological-oceanographic investigations in the eastern tropical Pacific Ocean began with expeditions Eastropic (1955) and Scope (1956). Much attention was given on these expeditions to distributions of primary productivity, standing crop of chlorophyll *a*, and standing crop of zooplankton (Holmes, Schaefer, and Shimada, 1957; Holmes and others, 1958); these observations were intended to contribute to the under-

standing of the ecology of the tunas of the region and to oceanographic knowledge. Much of this work was done by the Scripps Institution of Oceanography, University of California. In 1957 the Institution's work in this field was put on a continuing basis in the STOR Program, with support from the Bureau of Commercial Fisheries. As a result, several more cruises were made in the eastern tropical Pacific, which differed from Eastropic and Scope in that measurements of an additional biological property, namely standing crop of micronekton, were made routinely.

Micronekton, a term occasionally found in marine biological literature (e.g., Marshall, 1954), is here defined as the assemblage of actively swimming fishes, crustaceans, and cephalopods, ranging from about 1 cm. to 10 cm. in greatest dimension. In this paper it means all fishes, crustaceans, and cephalopods caught by a net designed to sample

¹ Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

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Some preliminary results of this research were given in a symposium at the Tenth Pacific Science Congress of the Pacific Science Association, held at the University of Hawaii in August and September 1961. The symposium was entitled "Factors affecting the behavior of predaceous marine fishes, especially sharks."

the animals mentioned above. The catches included some animals smaller than 1 cm. or larger than 10 cm., but they probably contributed less than 5 percent of the total volume. Micronekton and zooplankton overlap in catches in plankton nets—for instance, euphausiids occur in both.

The reasons for measuring the standing crop of micronekton and each of its main components were as follows:

(1) Because tunas feed on micronekton, a knowledge of its distribution might help to explain the variable distribution of tunas in the eastern tropical Pacific.

(2) Comparisons of net-caught and tuna-caught micronekton (the latter from tuna stomachs) might be of value in the study of feeding behavior of tunas, especially in the matter of possible selection of organisms.

(3) Food-chain relations in the ocean have had much physiological and statistical study between the producer and herbivore trophic levels, but comparatively little study has been made between those levels and the carnivore levels. This deficiency seems to reflect a shortage of data on standing crops of oceanic carnivores, especially primary carnivores such as small fish and cephalopods which are eaten by secondary carnivores; where such data are available, they generally refer to a few species for which there are commercial fisheries (e.g., herring, *Clupea harengus*). Because good programs of measurement of phytoplankton and zooplankton were already operating in the eastern tropical Pacific, it seemed worthwhile to measure micronekton as well.

This paper presents a summary of most of the micronekton data obtained before 1964 in the eastern tropical Pacific and analyzes them in reference to distribution and relation to contents of stomachs of tuna. Statistical analysis in reference to food-chain relations has been made, in part, elsewhere (Blackburn, 1966a).

MATERIAL AND METHODS

The net-caught micronekton obtained in the eastern tropical Pacific and adjacent waters was taken in the following three ways:

(1) In standard (identically made) night hauls of a net called the 1.5-m. (or 5-foot) net (described below), at a ship speed of 5 knots.

(2) In nonstandard night or day hauls of the same net.

(3) In hauls of a net called the high-speed net, described below, made at the ordinary cruising speed of the vessel (which ranged from about 9 to 12 knots, for the different vessels used).

The most useful quantitative data are those from standard night hauls, and this paper is concerned almost entirely with them. They were obtained on the following cruises: TO-58-1 (or SCOT), April-June 1958; TO-59-1, January-February 1959; TO-59-2, August-September 1959; TO-60-1; May 1960; TO-60-2 (or STEP-1), September-December 1960; and TO-61-1, March-April 1961 (see figs. 1 and 2 for areas covered). The total number of standard night hauls from all these cruises was 131 (see table 1). In addition, brief mention is made of 38 standard hauls (19 night, 19 day) made on cruise TO-62-1 (or TEMPO), August 1962, off Acapulco, Mexico. The hauls in this series (see table 2) are separated from the main data because they were made close together in space and time; they were not comparable with the other 131 hauls which were much more widely distributed in space and time in the eastern tropical Pacific.

Nonstandard hauls, occasionally made by day or night, are not discussed. The high-speed hauling method, and some data from it, are briefly described and evaluated.

1.5-M. NET: DESCRIPTION, OPERATION, AND PERFORMANCE

Figure 3 shows the 1.5-m. net. It is in the form of an elongated pyramid; the base (the mouth of the net) is 1.5 m. square, and the measurement from the center of the base to the apex is 5.8 m. The base or mouth is surrounded by a narrow selvage laced to a square frame of galvanized iron, to which the towing bridles and depressors are attached. The apex is open and the opening contains a brass fitting set in canvas, by which a cod end (not included in the 5.8-m. length) can be attached. The material and mesh of the net (excluding selvage and cod end) are uniform throughout: Marion Textiles 467-pattern nylon netting,³ with meshes approximately oblong and measuring about 5.5 mm. by 2.5 mm. The long

³ Mention of manufacturer does not imply endorsement of the product.

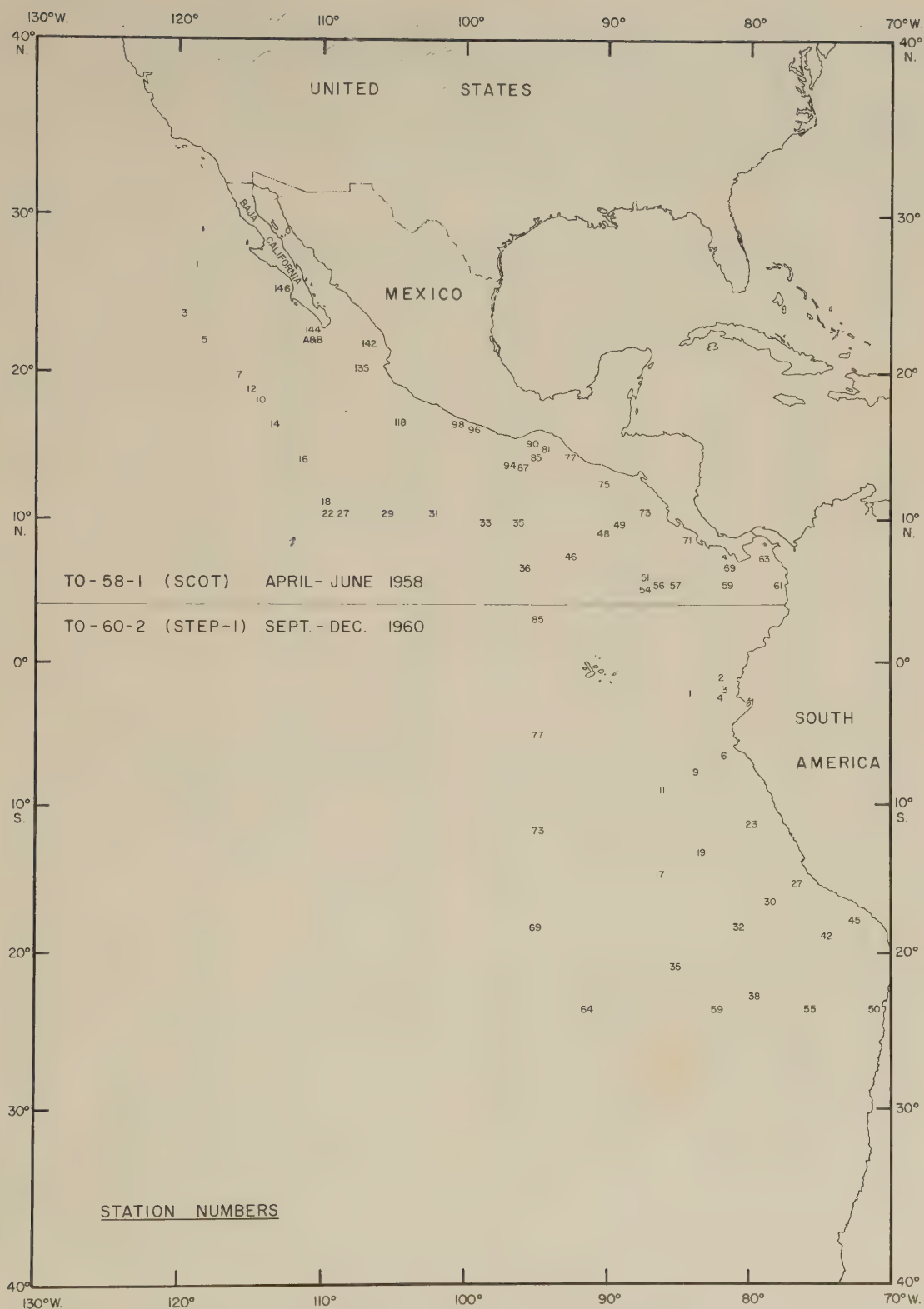


FIGURE 1.—Serial numbers and positions of stations at which standard night micronekton hauls were made on cruises TO-58-1 and TO-60-2.

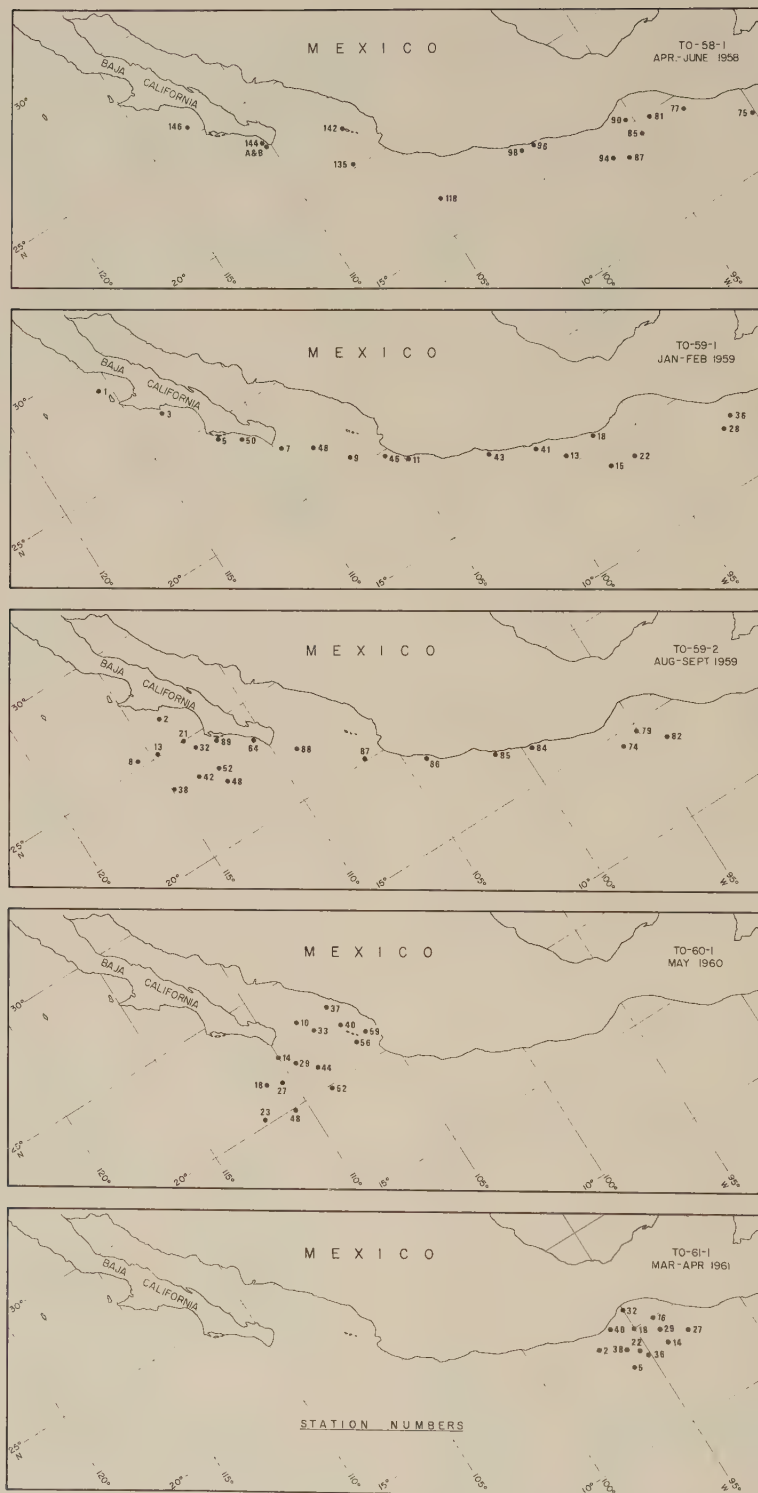


FIGURE 2.—Serial numbers and positions of stations at which standard night micronekton hauls were made in waters adjacent to Mexico and Guatemala, on cruises prior to 1962.

TABLE 1.—Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5-m. net

[Asterisk means that the station did not fall within the area stated, but has been included in it]

Station ¹ number	Date	Area ²	Time ³	Depth ⁴	Actual volumes				Standardized volumes			
					Fishes	Crusta- ceans	Cepha- lopods	Total	Fishes	Crusta- ceans	Cepha- lopods	Total
A. Cruise TO-58-1 (SCOT): April-June 1958												
		Number	Minutes	M.	Ml.	Ml.	Ml.	Ml.	Ml./10 ³ m. ³	Ml./10 ³ m. ³	Ml./10 ³ m. ³	Ml./10 ³ m. ³
1	Apr. 25	15	65		26	67	3	96	1.5	3.8	0.2	5.5
3	26	15	65		44	104	<1	148	2.5	5.9	<.1	8.4
6	27	15	64		17	35		52	1.0	2.0		3.0
7	28	*02	64		55	28		83	3.2	1.6		4.8
10	28	02	65		47	13	<1	60	2.7	.7	<.1	3.4
12	29	02	75		2	471		473	.1	23.2		23.3
14	30	*02	64		109	5	3	117	6.3	.3	.2	6.8
16	1	*02	72		45	4	3	52	2.3	.2	.2	2.7
18	2	*09	65		18	13	2	33	1.0	.7	.1	1.8
22	2	09	65		1	9	2	12	.1	.5	.1	.7
27	3	09	65		14	10	2	26	.8	.6	.1	1.5
29	5	16	64		64	10	9	83	3.7	.6	.5	4.8
31	6	16	64		63	18	8	89	3.6	1.0	.5	5.1
33	7	16	65		131	63	10	204	7.4	3.6	.6	11.6
35	8	16	65		57	44	9	110	3.2	2.5	.5	6.2
36	9	16	64		147	56	19	222	8.5	3.2	1.1	12.8
46	12	16	64		152	69	7	228	8.8	4.0	.4	13.2
48	13	05	63		189	70	43	302	11.1	4.1	2.5	17.7
49	13	05	64		189	62	130	381	10.9	3.6	7.5	22.0
51	15	11	69		59	52	11	122	3.1	2.8	.6	6.5
54	15	11	65		87	58	3	148	4.9	3.3	.2	8.4
56	16	11	64		93	82	15	190	5.4	4.7	.9	11.0
57	17	11	63		60	58	9	127	3.5	3.4	.5	7.4
59	18	12	62		106	126	19	271	6.3	8.7	1.2	16.2
61	19	10	65		91	143	7	241	5.2	8.1	.4	13.7
63	20	10	67		398	113	72	583	22.0	6.2	4.0	32.2
69	24	*12	64	90	147	113	20	280	8.5	6.5	1.2	16.2
71	25	05	66	105	110	68	21	199	6.2	3.8	1.2	11.2
73	26	05	64	80	183	68	95	346	10.6	3.9	5.5	20.0
75	27	05	63	83	196	111	62	369	11.5	6.5	3.7	21.7
77	28	04	60	100	319	58	90	467	19.7	3.6	5.5	28.8
81	29	04	71		533	72	124	729	27.8	3.7	6.5	38.0
85	30	04	66	110	168	88	88	344	9.4	4.9	4.9	19.2
87	30	04	68		109	28	18	155	5.9	1.5	1.0	8.4
90	31	04	66	72	150	17	62	229	8.4	.9	3.5	12.8
94	1	04	65	72	147	11	20	178	8.4	.6	1.1	10.1
96	2	04	65	115	221	36	10	267	12.6	2.0	.6	15.2
98	6	04	65	100	248	23	30	301	14.1	1.3	1.7	17.1
118	11	04	64	83	211	18	19	248	12.2	1.0	1.1	14.3
135	14	03	65	72	201	31	41	273	11.4	1.8	2.3	15.5
142	16	03	64		320	62	35	426	19.0	3.6	2.0	24.6
144A	17	01	65		266	67	6	339	15.2	3.8	.3	19.3
144B	17	01	65		206		3	1,814	11.7	91.3	.2	103.2
146	18	01	63		7	1,924	<1	1,931	.4	112.9	<.1	113.3

B. Cruise TO-59-1: January-February 1959

1	Jan. 17	01	48	99	161	379		540	12.4	29.2		41.6
3	17	01	47	90		102		102		8.0		8.0
5	18	01	40	81	<1	358	<1	358	<.1	33.1	<.1	33.1
7	20	03	48	86	150	11	1	162	11.6	.8	.1	12.5
9	21	03	49	88	73	12	9	94	5.5	.9	.7	7.1
11	22	03	44	90	93	6	8	107	7.8	.5	.7	9.0
13	26	04	50	75	97	90	8	195	7.2	6.6	.6	14.4
15	27	04	53	80	125	66	8	199	8.7	4.6	.6	13.9
18	28	04	40	77	97	258	17	372	9.0	23.8	1.6	34.4
22	30	04	34	92	60	79	<1	139	6.5	8.6	<.1	15.1
28	8	05	47	78	120	54	29	203	9.4	4.3	2.3	16.0
36	14	05	49	82	90	53	61	204	6.8	4.0	4.6	15.4
41	16	04	48	81	50	269	19	338	3.9	20.7	1.5	26.1
43	17	04	45	79	101	39	20	160	8.3	3.2	1.6	13.1
46	20	03	52	73	68	15	16	99	4.8	1.1	1.1	7.0
48	20	03	46	83	66	22	11	99	5.3	1.8	.9	8.0
50	21	01	50	94	20	807		827	1.5	59.7		61.2

See footnotes at end of table.

TABLE 1.—Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5-m. net—Continued

Station ¹ number	Date	Area ²	Time ³	Depth ⁴	Actual volumes				Standardized volumes			
					Fishes	Crusta- ceans	Cepha- lopods	Total	Fishes	Crusta- ceans	Cepha- lopods	Total
C. Cruise TO-59-2: August-September 1959												
2	Aug. 15	01	52		60	1,187		1,247	4.3	84.5		88.8
8	16	*01	48		60	2,262	<1	2,322	4.6	174.4	<.1	179.0
13	17	01	49	115	18	779		797	1.4	58.8		60.2
21	19	01	49	85	42	907	1	950	3.1	68.5	.1	71.7
32	22	01	36	84	306	2,500	<1	2,806	31.5	257.0	<.1	288.5
38	24	01	44	82	92	637	3	732	7.7	53.6	.3	61.6
42	24	01	43	80	59	1,585		1,644	5.1	136.3		141.4
52	26	01	49	99	81	1,552	<1	1,633	6.1	117.2	<.1	123.3
58	27	01	46	93	149	530	9	688	12.0	42.6	.7	55.3
64	28	01	58	85	3	19	5	27	.2	1.2	.3	1.7
74	Sept. 8	04	44	85	85	11	10	106	7.2	.9	.8	8.9
79	10	04	46	81	100	18	19	137	8.1	1.4	1.5	11.0
82	11	05	49	91	81	37	25	143	6.1	2.8	1.9	10.8
84	13	04	47	90	267	82	16	365	21.0	6.4	1.3	28.7
85	15	04	51	84	203	34	14	251	14.7	2.5	1.0	18.2
86	16	03	49	91	98	8	39	145	7.4	.6	2.9	10.9
87	17	03	42	77	44	14	6	64	3.9	1.2	.5	5.6
88	18	03	48	80	122	250	8	380	9.4	19.3	.6	29.3
89	19	01	42	89	1	13	2	16	.1	1.1	.2	1.4
D. Cruise TO-60-1: May 1960												
10	May 6	08	52	160	26	110		136	1.9	7.8		9.7
14	7	03	36	150	7	5	<1	12	.7	.5	<.1	1.2
18	8	01	30	145	9	72		81	1.1	8.9		10.0
23	9	01	35	91	21	6		27	2.2	.6		2.8
27	10	01	25	114	34	56	<1	90	5.0	8.3	<.1	13.3
29	11	03	39	93	9	5		14	.8	.5		1.3
33	12	03	45	91	67	11		78	5.5	.9		6.4
37	13	08	44	122	338	14	11	363	28.4	1.2	.9	30.5
40	15	03	44	95	70	32		102	5.9	2.7		8.6
44	16	03	45	114	40	26	9	75	3.3	2.1	.7	6.1
48	17	02	43	109	29	10	3	42	2.5	.9	.2	3.6
52	18	03	43	110	77	8	2	87	6.6	.7	.2	7.5
56	19	03	37	120	14	9		23	1.4	.9		2.3
59	20	03	43	150	60	1,532	4	1,596	5.2	131.8	.3	137.3
E. Cruise TO-60-2 (STEP-1): September-December 1960												
1	Sept. 27	17	36		29	20	2	51	3.0	2.0	.2	5.2
2	30	06	52		148	34	11	193	10.5	2.4	.8	13.7
3	Oct. 1	06	62		126	53	8	187	7.5	3.2	.5	11.2
4	2	06	53		151	29	3	183	10.5	2.0	.2	12.7
6	8	06	50		166	449	2	617	12.3	33.2	.1	45.6
9	10	*06	45		113	50	22	185	9.3	4.1	1.8	15.2
11	11	11	48		83	15	3	101	6.4	1.2	.2	7.8
17	15	17	51		26	27	6	59	1.9	2.0	.4	4.3
19	16	17	51		52	11	8	71	3.7	.8	.6	5.1
23	17	17	49		94	40	4	138	7.1	3.0	.3	10.4
27	29	14	52		19	124	1	144	1.4	8.8	.1	10.3
30	30	*14	47		28	55	<1	83	2.2	4.3	<.1	6.5
32	31	18	51		20	4	3	27	1.5	.3	.2	2.0
35	1	18	51		6	21	2	29	.4	1.5	.2	2.1
38	3	18	57		10	60	4	74	.6	3.9	.3	4.8
42	5	14	49		29	3	7	39	2.2	.2	.5	2.9
45	7	14	52		86	16	28	130	6.1	1.1	2.0	9.2
50	18	18	54		56	34	<1	90	3.8	2.3	<.1	6.1
55	19	18	49		26	170	<1	196	2.0	12.8	<.1	14.8
59	22	18	50		37	19		56	2.7	1.4		4.1
64	24	18	49		16	1	2	19	1.2	1.1	.1	1.4
69	27	18	45		17	13	2	32	1.4	1.1	.1	2.6
73	29	17	49		64	2	<1	66	4.8	.2	<.1	5.0
77	Dec. 2	17	49		78	7	3	88	5.9	.5	.2	6.6
85	4	16	49		68	11	8	87	5.1	.8	.6	6.5

See footnotes at end of table.

TABLE 1.—Actual volumes and standardized volumes for fishes, crustaceans, cephalopods, and total micronekton from 131 standard night hauls of a 1.5-m. net—Continued

Station ¹ number	Date	Area ²	Time ³	Depth ⁴	Actual volumes				Standardized volumes				
					Fishes	Crusta- ceans	Cepha- lopods	Total	Fishes	Crusta- ceans	Cepha- lopods	Total	
F. Cruise TO-61-1: March-April 1961													
2.....	Mar. 17..... 19..... 22..... 23..... 24..... 29..... Apr. 1..... 2..... 3..... 4..... 6..... 7.....	04	53	-----	83	30	8	121	5.8	2.1	.5	8.4	
5.....		04	50	-----	177	59	96	332	13.1	4.4	7.1	24.6	
14.....		05	51	-----	142	48	32	222	10.3	3.5	2.3	16.1	
16.....		04	50	-----	94	432	5	531	6.9	32.0	.4	39.3	
18.....		04	49	-----	116	50	22	188	8.7	3.8	1.7	14.2	
22.....		04	49	-----	138	20	40	198	10.4	1.5	3.0	14.9	
27.....		05	49	-----	43	43	15	101	3.2	3.2	1.2	7.6	
29.....		04	51	-----	69	55	26	150	5.0	4.0	1.9	10.9	
32.....		04	49	-----	84	32	4	120	6.3	2.4	.3	9.0	
36.....		04	49	-----	81	30	54	165	6.1	2.3	4.1	12.5	
38.....		04	49	-----	87	22	18	127	6.6	1.7	1.3	9.6	
40.....		04	49	-----	36	7	36	79	2.7	.5	2.7	5.9	
Total, all cruises.....					12,756	25,240	2,008	40,004					

¹ See figure 1 for location of stations.
² See figure 5 for location of areas.

³ Duration of haul.
⁴ Maximum depth of haul measured by bathythermograph.

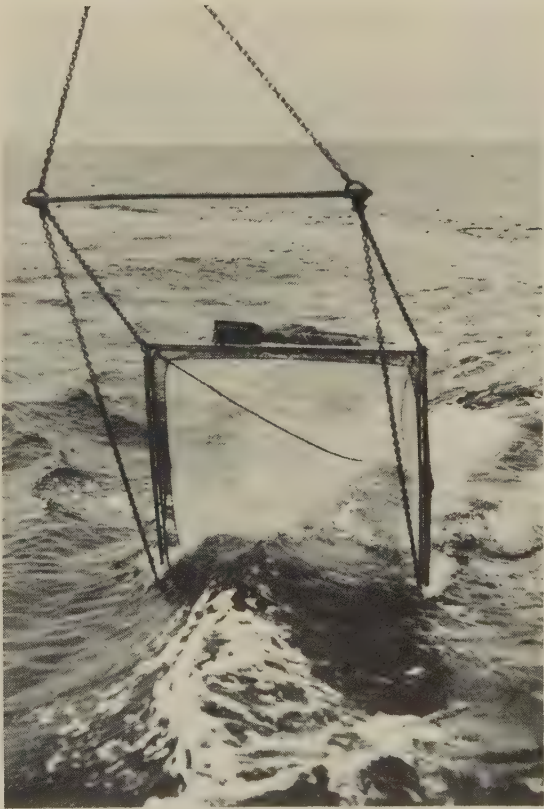
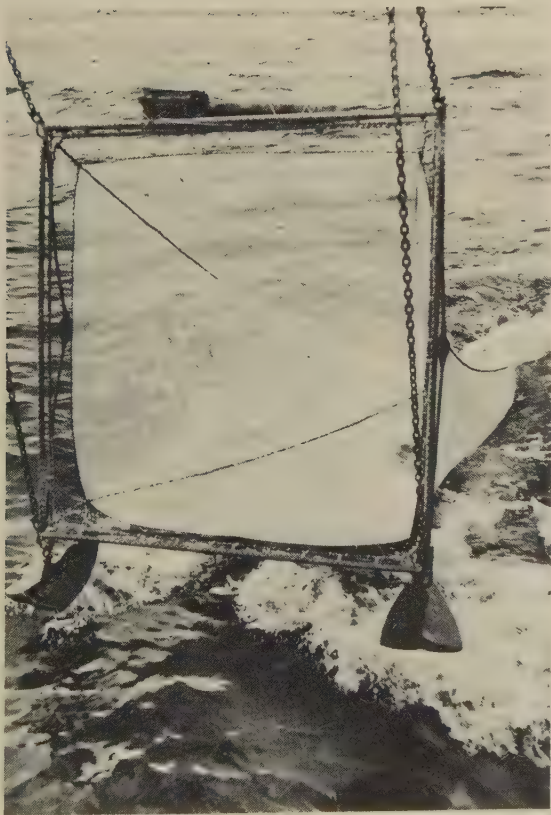


FIGURE 3.—Views of the 1.5-m. net, showing attachment of towing bridles, depressors, and bathythermograph (along upper side of square frame).

axis of the mesh is parallel to the long axis of the net. The ratio of total filtering area to area of mouth aperture (area of nylon thread included in the filtering area) is about 7.6:1. The detachable cod end is made of 56XXX nylon or silk grit gauze, with mesh apertures 0.31 mm. wide; the choice of this material was dictated purely by convenience (the same type of cod end was routinely used on the same cruises for collecting zooplankton). A larger mesh might have served equally well. Lengths of 6-mm. galvanized-iron welded-link chain are attached at one end to the four corners of the square frame and at the other end (in pairs, right side and left side) to the ends of a 1.5-m. galvanized-iron bar of 25-mm. diameter. Two similar chain bridles from the ends of the bar are attached to a swivel at the end of the 10-mm. towing wire rope. The arrangement and approximate lengths of the chain bridles are shown in figure 3. One sinker was attached to each bottom corner of the square frame; two 45-kg. cylindrical iron weights were used during cruise TO-58-1, but these were replaced by two 20-kg. bronze streamlined depressors during the other cruises.

When the 45-kg. weights were used, the hauling operation was as follows: 450 m. of the 10-mm. wire rope were paid out at 25 m./min. and then immediately retrieved at 10 m./min., all at a ship speed of 5 knots. The haul, thus, took about 63 min. (in practice there was some variation from the desired winching speeds—see table 1). It was found, by attaching a bathythermograph to the frame of the net, that the maximum depth ranged from 72 to 115 m. and averaged 90.2 m. (12 hauls). When the 20-kg. depressors were used, 350 m. of wire were paid out and retrieved at the same winch and ship speeds, for a total hauling time of about 49 min.; the maximum depth ranged from 73 to 160 m. and averaged 95.5 m. (48 hauls). Because the difference between the means is small, the two types of operation have been considered comparable except for the time; the second type has been continued routinely, and the catches from both types of hauls have been considered to represent broadly the quantity and quality of micronekton present at night that can be caught by the net in the upper 90 to 95 m. of ocean. The actual depths, where obtained by bathythermograph, are listed in table 1. The depressors were,

as expected, more effective in sinking the net than the much heavier cylindrical weights. A sampling depth of 90 to 95 m. would be expected with the Isaacs-Kidd midwater trawl also, if used on 350 m. of cable at a towing speed of 5 knots, according to tests made by Aron, Ahlstrom, Bary, Bé, and Clarke (1965).

No attempt was made to use a flowmeter in the net routinely, because it was thought that it might prevent the entry of some of the micronekton. Flowmeters were used twice to estimate the filtration coefficient of the net by making successive tows in a precisely identical manner, and of precisely the same duration, first with a flowmeter in the mouth of a fully rigged net, and then with the net removed and only flowmeter, frame, bridles, and depressors remaining. The ratio of flowmeter readings was 0.757 on the first trial and 0.738 on the second trial (3 years later). The net, used as described, apparently filters 74 to 76 percent of the water available (product of net-mouth area in square meters and distance towed in meters). Because the two estimates of the filtration coefficient are so close, the one first obtained, which had already been used to calculate volume of water strained on many of the hauls, was used for all. Water was available for filtration at the rate of 1,000 m.³ every 2.79 min. at a speed of 5 knots; the rate of actual filtration was estimated by the coefficient 0.757 to be 1,000 m.³ every 3.69 min. By dividing the measured volume by the total number of minutes for the haul and multiplying by 3.7, the micronekton was standardized to volume per 1,000 m.³ of water strained (see table 1).

The most important feature of this net is the mesh size, which retains most of the micronekton and releases most of the zooplankton, and, more importantly, is uniform throughout the net. This uniformity gives the standardized volumes a much more precise biological meaning than would be possible for similar measurements with a mixed-mesh net; some parts of a mixed-mesh net permit more escapement of organisms than other parts. Aron (1959, 1962a, 1962b) admitted this problem in relation to the Isaacs-Kidd midwater trawl, which has larger meshes near the mouth than near the cod end (as do most other nets and trawls hitherto used for catching micronekton and zooplankton). King and Iversen (1962), who used the Isaacs-Kidd and other trawls, observed that

"The nature of the trawling gear * * * did not permit or justify an exact quantitative evaluation of the catch." The Isaacs-Kidd and similar mixed-mesh midwater trawls seem to be much more useful for qualitative than for quantitative sampling. Percy and Laurs (1966) used an Isaacs-Kidd trawl lined with material of uniform small mesh size (5 mm. square).

The main difficulty with the 1.5-m. net is that some organisms, presumably the larger and more mobile ones—e.g., flying fish (Exocoetidae)—probably avoid the net or escape through the mouth after entry; doubtless similar escapement also occurs from the Isaacs-Kidd trawl and others of similar size. Apart from such unknown losses, standardized volumes from the 1.5-m. net estimate real concentrations of micronekton in the water.

The 1.5-m. net has proved to be easy to operate; it can be fished by two men, plus a winchman, except in rough weather or heavy swells, when it is prudent to employ a third man. Specimens caught generally are in good condition.

The standard 1.5-m. net hauls were made at night—usually about midnight—because most kinds of micronekton are more readily caught in near-surface waters by night than by day (Aron, 1959, 1962a; King and Iversen, 1962; Percy, 1964; and table 2 of this paper). It would be necessary to lower the net to greater depths, at appreciably greater cost in ship time, to obtain similar samples in the daytime. Percy (1964) found no obvious difference in numbers of mesopelagic fishes caught with the Isaacs-Kidd midwater trawl at different times of night at the same station, and I assume that time of night is equally unimportant for the other animals sampled.

HIGH-SPEED NET: DESCRIPTION, OPERATION, AND PERFORMANCE

The high-speed net is an elongated cone with a base (the mouth of the net) 70 cm. in diameter and measures 2.6 m. from the center of the base to the apex (fig. 4). The base or mouth is surrounded by a narrow selvaige laced to a circular frame of galvanized iron. The opening at the apex

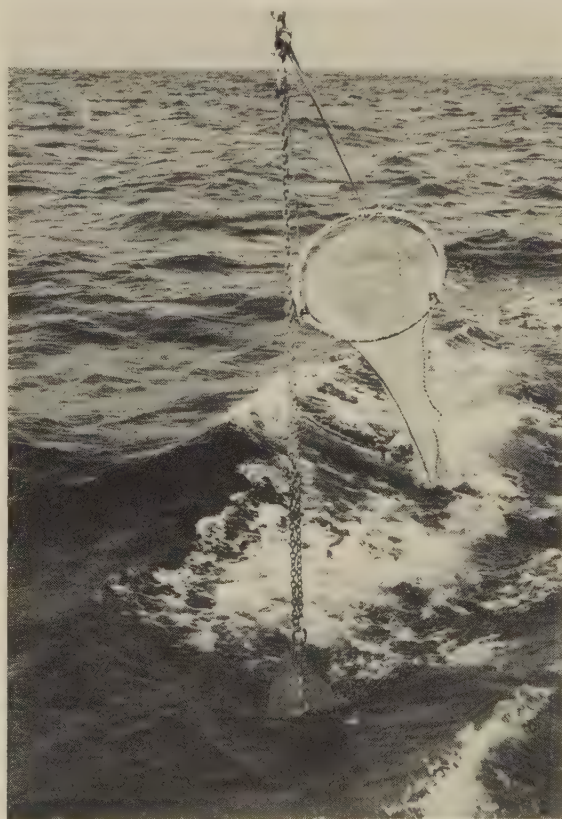


FIGURE 4.—Views of the high-speed net, showing attachment of towing bridles and depressor.

contains a brass fitting set in canvas, by which a cod end (the same cod end as for the 1.5-m. net; length not included in the 2.6-m. length of net) can be attached. The material and mesh of the net are the same as for the 1.5-m. net and uniform throughout. The ratio, total filtering area to mouth-aperture area (area of nylon thread included in the filtering area), is about 7.5:1. Three plastic cord bridles extend from the circular frame to the swivel at the end of the towing wire (the same as for the 1.5-m. net); one 20-kg. bronze streamlined depressor is also attached to this swivel on a 2.4-m. length of 6-mm. welded-link chain so that it is below the net when both are in the water.

This net has been used only for horizontal hauls at cruising speeds of 9 to 12 knots, with 50 m. of towing wire out. Under these conditions it is about 10 m. below the surface (as determined with an attached bathythermograph). Most hauls with the high-speed net were made at night, because daytime hauls caught little. Generally, only one man and a winchman were required to operate the net; when other operations were compatible, the normal routine was to tow the net about 2 or 3 hours, haul it up to change the cod ends, and put it out again for a similar tow, all without stopping or slowing the ship. The main difficulties (in order of magnitude) were that (a) other operations often did not permit a reasonably uniform time for each tow, (b) the organisms caught were generally in poor condition (with much flesh lost) when removed from the cod end, and (c) wear generally forced replacement of the net after about 1,000 to 1,500 nautical miles (1,850 to 2,780 km.) of towing (sooner, if catches were heavy).

The filtration coefficient (at 9 knots), estimated twice in 3 years in the same way as described for the 1.5-m. net, was 0.938 for the first trial and 0.811 for the second. This coefficient shows that the high-speed net filters more efficiently at 9 knots than the 1.5-m. net does at 5 knots; the two estimates do not agree as well as the two for the 1.5-m. net.

The value of 0.938 for the coefficient had been used to standardize the volumes of catches from two cruises before the 0.811 value was determined; these standardized volumes have been retained for the present, since there is no reason to prefer the second value of the coefficient to the first. Volumes were standardized by dividing actual volumes by

the number of minutes for the haul and multiplying by 10.0, since I calculated (from the 0.938 coefficient) that the net actually strained 1,000 m.³ of water every 9.96 minutes. The standardized volumes are not tabulated in this paper, but the actual volumes for cruises TO-59-2 and TO-60-2 have been listed elsewhere (Blackburn, Griffiths, Holmes, and Thomas, 1962; Scripps Institution of Oceanography, 1961), and some of the standardized volumes for those cruises are summarized here in figures 18 and 19.

TREATMENT OF COLLECTED MATERIAL

The net catches were preserved in 10 percent buffered formalin (4 percent formaldehyde). All organisms except sea snakes, which are dangerous to handle, were included. Later I sorted the material (a few days later for the major cruises TO-58-1 and TO-60-2; up to 3 years later for other cruises) into four components—fish, crustaceans, cephalopods, and others—and measured the displacement volume of each of the first three components. I also noted the taxonomic composition of each component, by volume or number of individuals, as far as I was able. The fourth component consisted of tunicates, medusae, siphonophores, chaetognaths, heteropods, and pteropods, which are not considered to be micronekton and are not significant in the diets of tropical tunas.

Subsequently, the fish, crustaceans, and cephalopods were sorted, generally to family or, for cephalopods, to genus and species. Displacement volumes of these groups for each haul were then measured (for large samples of fish and crustaceans) or estimated from the number and size of the organisms (for cephalopods, and small samples of fish and crustaceans), and these measurements were reconciled with the original measurements of the three main groups. Occasionally the reconciliation was impossible as a result of unauthorized removal of specimens between the first and the second sorting; the taxonomic composition of the catch by volume was then estimated from the notes made at the first sorting and, rarely, from the catch at another station adjacent in space and time. I realize that the measurements of minor groups are not entirely free from error, but the errors are small and scattered and mostly affect the scarcer groups. The sorted material from these hauls has been catalogued and stored at the Scripps Institution of Oceanography.

CHANGES IN MICRONEKTON FROM DAY TO NIGHT ON SUCCESSIVE DAYS IN THE SAME AREA

Table 2 gives the standardized volumes from standard hauls made alternately about local noon and midnight during a 20-day period of tracking a drifting surface-current drogue off the coast of southern Mexico (cruise TO-62-1 or TEMPO, August 1962). The hauls were encompassed by a rectangle bounded by lat. 14°58.0' N. and 15°17.8' N. and long. 99°49.7' W. and 100°48.0' W.; the same body of surface water was sampled throughout the period. Table 2 shows the expected striking difference between noon and midnight volumes of total micronekton, which have ranges of 0.4 to 2.1 and 4.3 to 14.3 ml. per 1,000 m.³ respectively. The main reason for this difference is that several families of mesopelagic fishes—Myctophidae, Gonostomatidae, Stomiidae, Bathylagidae, and Melamphaidae—occurred frequently in midnight catches although they were practically unrepre-

sented in noon catches. Bregmacerotidae also occurred exclusively in the midnight catches, and Carangidae and Leptocephali were taken in larger numbers at midnight than at noon. The principal crustacean groups in this series of micronekton samples were hyperiid amphipods and stomatopod (squillid) larvae, both of which tended to be more abundant in the noon catch than in the midnight catch on any particular day. These groups were the most abundant in the noon samples, which contained comparatively few fishes. Cephalopods occurred in small, broadly similar, amounts in both noon and night samples.

The noon and night series are, thus, greatly different quantitatively and qualitatively; on the other hand, the hauls in each of these series have a great deal of similarity, especially between those made on consecutive days. Consecutive night hauls seldom differed in total volume by a factor of >2 and consecutive noon hauls seldom differed by a factor of >3. Consecutive samples in either series

TABLE 2.—Micronekton from standard 1.5-m. net hauls made alternately about local noon (D) and local midnight (N) during a 20-day drogue-tracking experiment on cruise TO-62-1 (TEMPO), August 11 to 30, 1962

[Asterisk means <0.1 ml. per 1,000 m.³]

Haul No.	D or N	Time (mi - utes)	Group (Ml./10 ³ m. ³)													Total micro-nekton
			Mycto-phids	Gono-stoma-tids	Lepto-cephali	Caran-gids	Stomi-atids	Bathyl-agids	Melam-phaidae	Bregma-cerotids	Other fishes	Hyper-ids	Squillid larvae	Other crusta-ceans	Cepha-lopods	
1.	D	55									0.3	0.3	(*)		0.1	0.7
2.	N	50	2.8	1.1	0.3			1.0	0.6	0.3	.3	.6		0.3	.3	7.6
3.	D	50	.1	.2							.1	1.4	(*)		.3	2.1
4.	N	50	8.9	.4	.2	2.0						.2	0.2	.1	.2	12.2
5.	D	50									.1	.2	.1			.4
6.	N	50	6.1	.7	.2				.1		.1	.2	(*)		.1	7.5
7.	D	49			.2						.1	.4	.1	(*)	.1	.9
8.	N	50	5.8	.2	1.5	(*)					.1	.1	(*)	.1	.1	7.9
9.	D	49			(*)						(*)	.1	.2	.1	.1	.8
10.	N	49	2.9	.3	1.7	(*)					(*)	.3	.1	.1		5.4
11.	D	49									.2	.2	(*)	.1	.6	1.1
12.	N	50	6.6	.6	.2						.1	.2	(*)	.1	.2	8.0
13.	D	49									.2	.7	.1	(*)	.2	1.2
14.	N	50	5.9	.5	2.0	.4					(*)	.7	(*)	.1	.1	9.2
15.	D	49		(*)	.1						.1	.7	.1	.1	.2	1.3
16.	N	47	7.3	2.2	2.2	1.6					.1	(*)	(*)	.1		13.5
17.	D	48			.1						(*)	.2	.1	.1	.1	.6
18.	N	50	6.3	.9	.8		0.4				.1	.2	(*)	.2	.4	9.3
19.	D	48										1.0	.1		.1	1.2
20.	N	49	.8	12.8	.1	(*)	.4			(*)	.1	(*)		.1	(*)	14.3
21.	D	49										.2	.2			.4
22.	N	49	2.9	1.3	.5	.8	.4		.1	(*)	.2	.1	(*)	.1	.1	6.5
23.	D	50			.1	.2					.1	.3	.1	.1	.3	1.1
24.	N	50	3.2	.9	.4		.7	.2	.8	.1		(*)	(*)	.1	(*)	6.4
25.	D	50			(*)	.4					.4	.2	.2	.1		1.3
26.	N	50	3.9	.3	.2		.3	.4	.7	.1	.1			.1	(*)	6.1
27.	D	49			(*)						(*)	.4	.2		.2	.8
28.	N	50	4.7	1.0	(*)	(*)	.3	.1			.1	(*)	.8		.2	6.4
29.	D	48									.1					1.4
30.	N	50	2.8	.9			.2	.4	.2	(*)	.1	.5	.7	.1	.1	4.7
31.	D	49			.1						.2			.1	(*)	1.6
32.	N	55	3.3	.5	.1		.2	.6	.1	(*)	.1	(*)	(*)	.1	.1	5.0
33.	D	49										.4	.3	.1	.1	.9
34.	N	50	5.7	1.0	.4		(*)	.3	(*)	.3	.1	(*)	(*)	.1	(*)	7.9
35.	D	49									(*)	.3	.2		(*)	.5
36.	N	50	3.3	.4	.2	(*)	.1	.2	.3	(*)	.1		(*)	(*)	.2	4.8
37.	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
38.	N	50	1.3	.7	.2		.8	.5	.4	.2	(*)	(*)		.2	(*)	4.3
39.	D	49											.2		.2	.4

¹ Haul omitted.

also did not differ greatly in taxonomic composition (table 2). These results were expected because all the catches were made in the same body of surface water. They suggest that the catches of the other, more isolated, single hauls listed in this paper are reasonably representative, both qualitatively and quantitatively, of the micronekton population sampled.

AREAL DISTRIBUTION OF MICRONEKTON BY TAXA

Table 1 gives the actual and standardized volumes of fish, crustaceans, and cephalopods for each of the 131 standard night hauls of the 1.5-m. net, excluding the special series mentioned in the previous section. It also gives the number, date, and area (see below) of each of the stations at which each haul was made.

The approximate position of each station is shown in figure 1 or figure 2. The actual positions of the stations are available from the following sources: cruise TO-58-1, Holmes and Blackburn, 1960; TO-59-1 and TO-59-2, Blackburn et al., 1962; TO-60-1, Scripps Institution of Oceanography, 1967; TO-60-2, Scripps Institution of Oceanography, 1961; TO-61-1, Blackburn, unpublished.

The stations were assigned to areas which are shown in figure 5. Areas 1 to 14 are those recognized by Alverson (1963a) in a study of the food of tropical tunas taken in the U.S. surface tuna fishery. Areas 15 to 18 enclose stations occupied farther offshore. No stations with micronekton hauls were occupied in areas 7 and 13; areas 11 and 12 have been combined in this paper; a few stations close to the boundaries of certain areas have been assigned to those areas for convenience.

For the 131 hauls, the actual total volumes were: 12,756 ml. of fish; 25,240 ml. of crustaceans; and 2,008 ml. of cephalopods; grand total, 40,004 ml. These numbers are given by taxa (including some species) and areas in table 3, which is the most convenient way of presenting the composition of the whole material. Some of these data are used in later sections (tables 8-15).

Although many families are listed in table 3, only 10, together with the Leptocephali of the suborder Apodes (Pisces) which have not been

classified to family, contributed more than 1 percent of the grand total; these 11 groups combined accounted for 93.4 percent (table 4). The Euphausiacea of table 3 are all members of the family Euphausiidae.

Table 5 gives standardized volumes of the principal fish and crustacean components of the micronekton as listed in table 4, for each station. The sum of volumes equals the standardized volumes for total fish and total crustaceans in table 1.

Figures 6 to 13 show distributions of standardized group volumes for the two most extensive cruises, TO-58-1 (SCOT) and TO-60-2 (STEP-1); figure 1 identifies the stations; the data are from tables 1 and 5. These cruises were made in the Northern Hemisphere in the northern spring and the Southern Hemisphere in the southern spring, respectively. The two space-time situations were comparable climatically; trade winds were declining in average strength from their seasonal maximum about late winter or early spring. A general similarity should, therefore, exist between the two situations in certain wind-connected upper-ocean features which affect the production and distribution of organisms. For instance, amount of coastal upwelling, mean depth of mixed layer, and mean velocity of westerly surface currents would all be expected to be declining, as a result of the decrease in the trade winds, in each situation. Because the two cruises were comparable in range of latitude from the Equator, and range of distance offshore, it is reasonable to combine biological data from both in the way that has been done in figures 6 to 13. These figures, then, give the best available picture of regional distribution of the standing crops of various kinds of micronekton over a large part of the eastern tropical Pacific, under comparable physical conditions.

Figures 6, 7, and 8 chart the distribution of fish, crustaceans, and cephalopods, respectively (data from table 1). They show clearly that the standing crop of each of these three components of the micronekton declines from onshore to offshore. Table 6 shows the magnitude of these changes.

This distribution is rather similar to that of standing crops of chlorophyll *a* and zooplankton in the same region (Brandhorst, 1958; Bennett, 1963; Forsbergh and Joseph, 1964; Blackburn, 1966b). Each of the three standing crops—chloro-

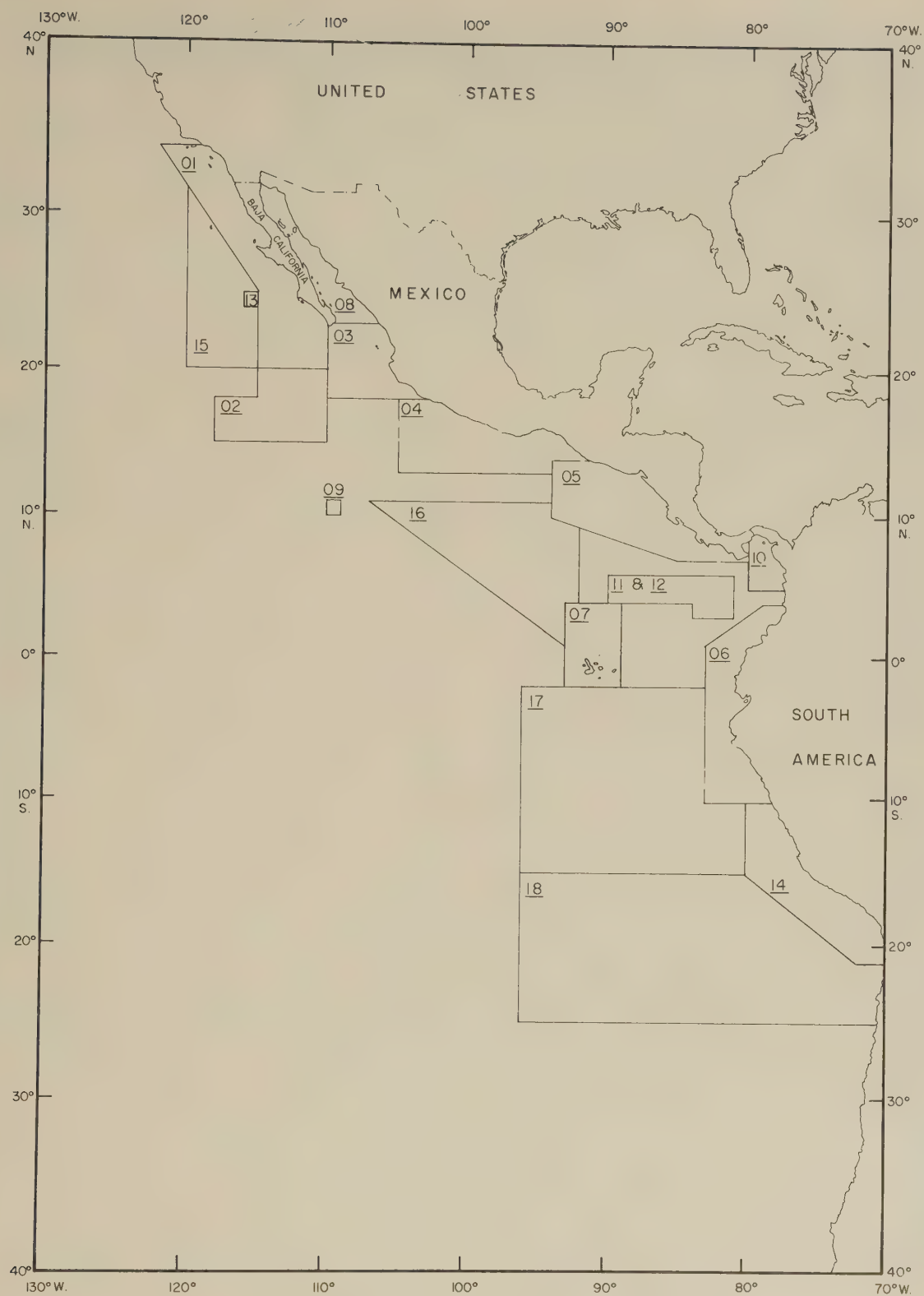


FIGURE 5.—Areas to which standard night hauls were assigned in table 1.

Table 3.—Actual volumes of micronekton from table 1, classified by taxa and areas

[Groups with <1 ml. for the combined areas are unlisted; asterisk means <1 ml. for a particular area. Abbreviations in the left-hand column signify: a.—adult, j.—juvenile, l.—larva, m.—megalocephalus, ph.—phyllosoma, po.—postlarva, pu.—puerulus, r.—remains, unid.—unidentified, z.—zooea; if no ontogenetic stage is specified, the adult stage, or a mixture of adults and younger stages is meant.]

Animals	Area Number																	Total
	01	02	03	04	05	06	08	09	10	11, 12	14	15	16	17	18			
CEPHALOPODA																		
Decapoda																		
Enoplateuthidae:																		
<i>Pterygoteuthis giardi</i>	7					6			15	8			4	6	3		49	
Do. j.	(*)								1				1	4	2		8	
<i>Pterygoteuthis</i> sp. j.			1														1	
<i>Abrollopsis morisi</i>	9	7	116	434	305	18	9		55	45	6	3	15	7			1,029	
Do. j.			5	24	7	4	2		3	5			1				51	
Do. l.			1		1												2	
<i>Abrollopsis</i> sp.			2	9	3						2					1	17	
Do. j.																1	1	
<i>Abrolia</i> sp.			2	13	5			1									21	
Do. j.													1				1	
Onychoteuthidae:																		
<i>Onychoteuthis banksi</i>				7	5												12	
Do. j.				11	1												12	
<i>Onychoteuthis</i> sp. j.					1												1	
Unid. Onychoteuthidae					1										1		1	
Do. j.				1	1												3	
Cranchiidae:																		
<i>Leachia eschscholtzi</i>	2	1	35	342	88	12		5		11	23		40	5	3		567	
Do. j.		(*)	8	15	7			(*)	(*)	2	2		3		2		39	
Do. l.					1										(*)		1	
<i>Leachia</i> sp.				2													2	
Do. j.			1	1	1												2	
<i>Pyrgopsis</i> sp.	(*)		1	3	4						1					1	10	
Do. j.	1		12	7	1						1						22	
<i>Liocranchia reinharti</i>									5								5	
Do. j.			1			1							1				3	
<i>Teuthowenta</i> sp.										2							2	
Do. l.					(*)	1											1	
Unid. Cranchiidae j.	(*)		1														1	
Do. l.				(*)	1								1				2	
Bathyteuthidae:																		
<i>Ctenopteryx sicula</i>					1					3							4	
<i>Ctenopteryx</i> sp.						2									1		3	
Octopodoteuthidae:																		
<i>Octopodoteuthis</i> sp.													1				1	
Ommastrephidae unid.	5				2												5	
Histioteuthidae unid.					2												4	
Unid. squid r.	2		3	20	72					1	(*)			1			99	
Do. j.					1						1						3	
Do. l.	(*)	(*)	(*)	2	1	1		(*)	(*)	(*)		(*)	2	1	(*)		7	
Octopoda																		
Tremoctopodidae:																		
<i>Tremoctopus</i> sp. j.	2																2	
Argonautidae:																		
<i>Argonauta</i> sp.		1			2												1	
Do. j.	1																3	
Amphitretidae:																		
<i>Amphitretus</i> sp.				5													5	
Do. j.				2													2	
Do. l.			(*)	1	2	(*)				(*)	(*)		(*)				3	
Total Cephalopoda	29	9	189	901	513	46	11	6	79	77	36	3	70	26	13		2,008	
CRUSTACEA																		
Isopoda	(*)	1	(*)	(*)	(*)													
Amphipoda																		
Gammaridea		(*)	(*)	(*)	(*)			2	(*)				3				5	
Hyperidea:																		
Phronimidae	4	2	13	33	24	5	2	2	1	13	2	(*)	8	6	6		121	
Phrosinidae	(*)	(*)	3	7	7	4		1	2	7			5	1	7		44	
Oxycephalidae	2	1	9	23	12	5	(*)	3	1	5	2		7	5	5		80	
Platyscelidae			2	7	7	4		(*)	(*)	1			7	(*)	(*)		28	
Paraphronimidae				3	5	(*)		(*)	1	5	2		3	3	2		24	
Vibilidae	3	4		7	6	(*)	(*)	1	1	3	2		(*)	3	4		40	
Scinidae	(*)	2	(*)	9		(*)	(*)	(*)	(*)	(*)	3		(*)	(*)	3		8	
Unid. Hyperidea	1	(*)	6	17	6	5		2	1	5	5		4	4	4		60	
Euphausiacea	1,528	38	265	91	101	438	104	6	23	163	170	6	71	29	250		3,283	
Decapoda																		
Sergestidae	8	1	17	82	181	40	2	2	49	138	2	4	92	27	10		655	
Do. po			2	(*)	5	(*)		1	(*)	(*)			3	2	2		15	
Penaeidae	1		1,516	(*)	20	46	4		(*)	(*)	3	1	8	28	16		1,651	
Do. z.	2	(*)	8	27	10	5	2		1	(*)			(*)	(*)			55	
Pasiphaeidae	277												4				281	
Oplophoridae				(*)		2									2		4	
Pandalidae	1					2							3	(*)	(*)		6	
Amphionidae l.	(*)			(*)	5	3		2	1	(*)			4	(*)	3		20	
Unid. Caridea			2	2													2	
Palinuridae ph.	2	1	4	13	10	(*)		1	(*)	7			8				46	
Do. pu.			2	8	(*)				1	1			(*)				12	
Galatheaidea:																		
<i>Pleuconodes planipes</i>	15,474	470	2									191					16,137	
Unid. Galatheaidea z & j.	(*)		1	15	(*)	3	1		1				(*)	(*)			20	
Porcellanidae z.	1	2	5	19	5	3		1	1	5	1		1	(*)	(*)	(*)	44	
Paguridae m.	(*)		6	17	6	(*)			1				(*)				35	
Hippidae z.	(*)		2	11	(*)						(*)		(*)	(*)	(*)		13	

Table 3.—Actual volumes of micronekton from table 1, classified by taxa and areas—Continued

Animals	Area Number																Total
	01	02	03	04	05	06	08	09	10	11, 12	14	15	16	17	18		
CRUSTACEA—Continued																	
Albuneidae z.	Ml. (*)	Ml.	Ml. 3	Ml. 23	Ml. 5	Ml. (*)	Ml. (*)	Ml.	Ml. (*)	Ml. (*)	Ml.	Ml.	Ml. 3	Ml.	Ml.		
Portunidae:																	34
Portunus affinis				830	37				130	65							1,062
Euphyllax dovii									1								1
Unid. Portunidae					4												4
Do. j.				1						(*)							1
Dorippidae z.	(*)		4	18	7	5	1		2	(*)			(*)	1	2	(*)	38
Unid. crab m.	3		8	36	8	5	1	2	1	6	2		1	2			75
Unid. decapod l.	4	1	9	25	8	5	2	2	1	6	5		4	3	4		79
Do. r.	(*)		2	(*)	(*)	(*)								(*)			2
Stomatopoda																	
Squillidae l.	33	8	164	228	109	32	5	4	31	45	2	3	32	5	(*)		701
Do. po. & a.	(*)		(*)	477	15												492
Unid. crustacea r.	3			12	11	(*)			6	21		1		3	4		61
Total Crustacea	17,347	531	2,059	2,034	614	615	124	32	256	509	198	206	271	122	322		25,240
PISCES																	
Albulidae l.				2		2											4
Gonostomatidae:																	
Vinciguerra spp.	125	62	272	322	84	33	14	6	60	28	17	19	48	69	22		1,181
Unid. Gonostomatidae	4	7	24	(*)	3								4	1	19		66
Stomatidae	16		20	42	46	10		2	53	31	(*)	5	18	27			270
Melanostomatidae				14	8								3				25
Astronesthidae l.																	1
Sternoptychidae	(*)			2	1	46		(*)	1	(*)				3	1	21	75
Idiacanthidae		3		55	45			1	6	34							144
Myctophidae	1,342	134	523	1,557	403	452	304	21	240	225	125	52	278	311	115		6,082
Bathylagidae	8		3	27	39	13			5	1	2		11	5	(*)		114
Paralepididae	1		2	13	6	4		(*)	8	1		(*)	1		1		37
Scopelarchidae	1		2	13	9	7	(*)	(*)						2	(*)		34
Synodontidae l.				1	1												1
Nemichthyidae	3			22	60	21				5							115
Apodes: leptocephali	89	78	651	2,030	558	96	30	2	97	199	2	7	294	(*)	6		4,139
Belonidae l.			1														1
Scomberesocidae j.											6						6
Hemirhamphidae l.						1											1
Exocoetidae j.			7														7
Gadidae l.			(*)			2								(*)			2
Bregmacerotidae	5	2	50	36	6				7	18			11				135
Trachypteridae l.													1				1
Regalecidae l.													2				4
Heterosomata po.	(*)			45	28	4	(*)			2			2				78
Holocentridae l.			1										1				1
Melamphalidae			5	20	4	4	16				1				1		51
Syngnathidae l.				2													2
Thunnidae po.	(*)		(*)	(*)	2				(*)								2
Trichiuridae po.						6				5							11
Gempylidae po.																	3
Coryphaenidae l.			(*)	2						(*)			(*)				2
Bramidae l.				(*)									1				1
Stromateidae	(*)		7	8	23		(*)			2			1				45
Carangidae	(*)			5	1	2			2		9			2	2		25
Serranidae j.			2	4	3				1	(*)				4	2		10
Pracanthidae l.				1	1												2
Callionymidae l.																	1
Scorpaenidae po.	(*)		3	15	5				3	1							27
Labridae po.	(*)		4	2	4			(*)		1			(*)				11
Blennidae l.			1							1							2
Ophidiidae l.			5	2	2	1				1							11
Balistidae l.	1																1
Ostraciidae j.		1															1
Tetraodontidae j.			1					1		1							3
Diodontidae j.				2													2
Unid. pisces			4	13	1								1				19
Total Pisces	1,595	287	1,588	4,256	1,343	704	364	33	489	552	162	87	682	426	188		12,756

TABLE 4.—Major components of the micronekton; actual volumes from table 3, for all areas combined

Family or suborder	Actual volume	Percentage of total volume
	<i>Ml.</i>	<i>Percent</i>
Enoploteuthidae.....	1,180	2.95
Cranchiidae.....	657	1.64
Euphausiidae.....	3,283	8.21
Sergestidae.....	670	1.68
Penaeidae.....	1,706	4.26
Galatheidæ.....	16,157	40.39
Portunidae.....	1,068	2.67
Squillidae (larvae).....	701	1.75
Squillidae (postlarvae and adults).....	492	1.23
Gonostomatidae.....	1,247	3.12
Myctophidae.....	6,082	15.20
Apodes (Leptocephali).....	4,139	10.35
All others.....	2,622	6.55
Total micronekton.....	40,004	100.00

phyll *a*, zooplankton, and micronekton—is positively correlated with the others in the area of cruise TO-58-1 (Blackburn, 1966a). The distributions reflect the fact that physical situations which lead to high production of organisms, namely upwelling and vertical mixing by wind over shoal pycnoclines, are better developed along the eastern sides than in other parts of tropical oceans, except along the Equator (Wooster and Reid, 1963; Wyrтки, 1966). Crops of chlorophyll *a* and zooplankton are fairly high in offshore waters along the Equator (Forsbergh and Joseph, 1964; Blackburn, 1966b); this paper presents no data on micronekton for those waters, but King and Iversen (1962) found more micronekton near the Equator than elsewhere in the central tropical Pacific. In nonequatorial offshore waters the pycnoclines lie deeper and mixed layers are thicker (Wyrтки, 1964b); the likelihood of chemical enrichment from below is diminished, and, if there is such enrichment, part of the resulting plant crop will be carried by mixing below the compensation depth.

The standing crop of micronekton is not uniformly high in the coastal region. It tends to be higher in some parts of the region than in others. The standardized volumes of total micronekton for the 40 onshore stations (table 6) range from 113.3 to 2.9 ml. per 1,000 m.³, and this group can be divided into an upper two deciles (8 stations) and a lower eight deciles (32 stations). Table 7 shows that the eight stations with the higher total volumes also had the higher mean volumes for each of three main components of the micronekton.

The eight stations with high volumes are numbers 49, 63, 77, 81, 142, 144B, and 146 of cruise

TO-58-1, and number 6 of cruise TO-60-2. With the possible exception of station 142, they all occur in localities which are known to be especially productive of organisms, as a result of physical processes which operate at or a few months prior to the season at which the micronekton was collected. Stations 144B and 146 occur in the coastal upwelling region off Baja California (Reid, Roden, and Wyllie, 1958; Blackburn, 1966b); stations 77 and 81 are in the Gulf of Tehuantepec where vertical mixing occurs over a shoal thermocline (Blackburn, 1962); station 49 lies in the "Costa Rica Dome" region where upwelling, from cyclonic flow, takes place (Wyrтки, 1964a; Holmes, MS.⁴); station 63 occurs in the coastal upwelling region of the Gulf of Panama (Forsbergh, 1963); and station 6 is in the coastal upwelling region off Peru (Wyrтки, 1963; Forsbergh and Joseph, 1964).

Station 142 is in the mouth of the Gulf of California, which is not known to be as biologically productive as the other areas just mentioned. The mixed layer is <20 m. thick in an average June, however (Wyrтки, 1964b) and was so when the station was occupied in June 1958; the possibility of chemical and biological enrichment, as a result of vertical mixing, therefore, exists. On the other hand, this station is very close to an island; the high volume of micronekton (mainly fishes, see table 1), therefore, may represent an "island effect."

The standing crop of cephalopod micronekton appears to diminish polewards from the tropics (fig. 8) even along the coast, but this trend does not hold with the fish and crustaceans.

Figures 9 to 13 show similar data, from table 5, for some of the major groups of fish and crustaceans. The distribution of myctophids (fig. 9), the largest group by volume among the fishes, is broadly similar to that of all fish (fig. 6). Standing crops decline from onshore to offshore, although not as markedly as crops of some of the other groups (table 6). Myctophids are also well represented in the micronekton off the west coast of the United States (Aron, 1962a; Percy, 1964) and in the central Pacific (King and Iversen, 1962); it is impossible to make close quantitative comparisons of standing crops from those regions with crops

⁴ Holmes, Robert W. A contribution to the physical, chemical, and biological oceanography of the northeastern tropical Pacific (Scripps Institution of Oceanography, University of California, 357 pp.).

TABLE 5.—Standardized volumes of the principal components of fish and crustacean micronekton in the hauls listed in table 1

[Asterisk means <0.1 ml. per 1,000 m.³; see table 1 for standardized volumes of total fish and total crustaceans]

Station number	Fish components				Crustacean components							
	Myctophids	Leptocephali	Gonostomatids	Others	Gala-theids	Euphausiids	Penaeids	Portunids	Sergestids	Squillid larvae	Squillid adults	Others
ML./10 ³ m. ³												
A. Cruise TO-58-1 (SCOT): April to June, 1958												
1	1.1	0.1	0.3	(*)	3.4	0.2	(*)		0.1	0.1		
3	1.4		.8	0.3	5.7	.1	(*)		.1	(*)		(*)
5	.4	.3	.2	.1	1.8	.1			(*)	(*)		0.1
7	1.6	.7	.9			1.4				(*)		.2
10	1.0	1.2	.5			.5			(*)	.1		.1
12		(*)	(*)		23.2				(*)			(*)
14	3.8	1.4	1.0	.1		.2			(*)	.1		(*)
16	.8	.8	.5	.2								.2
18	.9	(*)	.1	(*)		(*)			(*)	(*)		.5
22		.1	(*)	(*)		.2			(*)	(*)		.4
27	.3		.2	.2		.1			(*)			.4
29	1.4	1.3	.7	.3		.1			(*)	.1		.4
31	1.3	1.8	.3	.2		.2				.1		.5
33	2.8	4.0	.4	.2		.3			.1	.3		.7
35	2.0	.6	.3	.3		.7			2.3	.1		.4
36	4.3	3.3	.5	.4		1.6	0.3		1.3	.4		.6
46	2.9	3.5	.6	1.8		.9	.2		.3	.6		1.0
48	3.8	4.4	.5	2.4		.8	.1	0.2	1.3	.8		.7
49	3.5	2.3	1.7	3.4		.5	.2		.9	.8		1.2
51	1.1	1.1	.2	.7		.8	(*)		.9	.2		.9
54	2.0	2.1	(*)	.8		.7	.1		1.4	.4		.7
56	1.7	2.8	(*)	.9		1.8	(*)		1.4	.5		1.0
57	1.5	1.4	(*)	.6		.6	(*)		.8	.4		.9
59	2.7	2.3	.6	.7		3.5	(*)		.7	.8		.9
61	1.7	.1	1.4	2.0		.3	(*)		2.1	1.0		1.3
63	11.6	5.2	1.9	3.3		1.0	(*)		.8	.4		.3
69	4.0	1.8	.9	1.8		2.1	.1		1.1	1.9		.9
71	1.9	1.8	.3	2.2		.7	.8		2.3	1.0		.8
73	2.6	4.9	.7	2.4		1.4	(*)		.4	.2		.7
75	1.8	7.0	.9	1.8		.8	(*)		.4	.6		.7
77	2.2	14.4	2.2	.9		.7	(*)		.8	.8	(*)	1.4
81	7.0	16.4	2.1	2.3	(*)	.5	.1		.9	.8		1.2
85	3.8	3.5	.5	1.6		.5	(*)		.3	1.6		1.2
87	.5	4.9	.3	.2		.3	(*)		1.3	.6	1.5	1.0
90	5.2	2.4	.7	.1		(*)	(*)		.2	.3		.7
94	1.8	5.5	.9	.2		(*)	(*)		(*)	.2		.7
96	1.1	10.8	.2	.5		(*)	(*)		.1	.1	(*)	.5
98	6.4	4.6	2.2	.9		.1	(*)		.4	.5	.1	1.0
118	2.4	3.8	3.2	2.8		.1	(*)		.1	.3		.8
135	3.7	4.0	2.2	1.5		.7	(*)		(*)	.2		.7
142	1.0	12.7	3.1	2.2		.3	(*)		(*)	.5	(*)	.6
144A	10.2	4.0	.6	.4	.2	2.5	(*)		.2	2.3		.8
144B	9.4	.3	.9	1.1	89.9	1.1	(*)		(*)	.7		.4
146	.2	.1		.1	100.7	(*)	(*)		(*)	.2	(*)	12.2

B. Cruise TO-59-1: January to February, 1959

1	12.1		.2	.1	26.4	2.8			(*)	(*)		
3					8.0	(*)	(*)					
5			(*)		32.7	.3			(*)			.1
7	3.5	7.2	.8	.1	.2	(*)	(*)			.5		.1
9	1.9	2.3	.7	.6		.1	(*)		(*)	.5		.3
11	5.0	2.6	.2	(*)		(*)	(*)			.2		.3
13	4.8	2.3	.1	(*)		(*)	(*)			.1		.5
15	4.3	3.5	.1	.8		.3	(*)	5.7	.3	.1		.7
18	6.1	2.4	.1	.4		.2	(*)	3.5	(*)	.1		.7
22	1.4	4.4	.2	.5	1.6	.4	(*)	21.6		.9		1.1
28	2.9	4.7	.1	1.7	(*)	.4	(*)	3.5	(*)	.3		.9
36	2.3	2.3	.2	2.0		.7	(*)	.3	.3	1.3	(*)	2.0
41	1.8	1.7	.2	.2	(*)	.1	(*)		.7	1.6		1.0
43	4.0	4.1	.1	.1		.1	(*)	20.0	.5	.1		(*)
46	2.1	1.8	.3	.6	(*)	.1	(*)	1.7	(*)	.5		.9
48	.6	4.0	.5	.2		(*)	(*)		(*)	.4		.6
50	.8	.4	.3	(*)	55.1	3.6	(*)		(*)	1.0		1.0

TABLE 5.—Standardized volumes of the principal components of fish and crustacean micronekton in the hauls listed in table 1—
Continued

Fish components					Crustacean components							
Station number	Mycto- phids	Leptoce- phali	Gonosto- matids	Others	Gala- thoids	Euphau- sids	Penaëids	Portunids	Sergestids	Squilla larvae	Squilla adults	Others
C. Cruise TO-59-2: August to September, 1959												
2.	4.3		(*)	(*)	81.5	(*)						3.0
8.	4.6		(*)		165.3				(*)	(*)		.1
13.	1.2		.2		46.5	9.0						
21.	3.1		(*)		65.3	12.3			(*)	(*)		.6
32.	31.5		(*)		222.6	2.6			(*)	(*)	.1	.1
38.	7.0		.7	(*)	40.6	34.2			(*)	(*)		
42.	4.4	(*)	.7		132.5	13.0			(*)	(*)		(*)
52.	5.9		.2	(*)	107.6	3.8			(*)	(*)	.2	
58.	7.2	(*)	4.7	.1	20.0	9.4			(*)	(*)		.6
64.	.1	(*)		.1	(*)	22.0			(*)	(*)	.1	.7
74.	4.0	2.0	.2	1.0		.4	(*)				.2	.6
79.	2.3	4.8	.2	.8		.1	(*)		.1	.2	.7	.6
82.	3.4	1.5	.2	1.0		.2	(*)	1.1	.2	.5	.8	.8
84.	9.4	10.6	(*)	1.0		(*)	(*)	4.9	.1	.2	1.2	1.2
85.	10.2	3.3	(*)	1.2		.1	(*)	1.4	.1	.7	.2	.2
86.	4.9	2.0	(*)	.5		(*)	(*)		.1	.4	.7	.5
87.	3.6	.3	(*)	(*)		(*)	(*)		(*)	.7	.5	.5
88.	3.9	1.1	4.2	.2		18.1	(*)		(*)	.4	.8	.8
89.	(*)	.1	(*)	(*)		.3	(*)			.4	.4	.4
D. Cruise TO-60-1: May 1960												
10.	.4	.2	.1	1.2	.1	7.3	.3		(*)	.1	(*)	.1
14.	.2	.1	.1	.3	(*)	.2	.1		(*)	.1		.5
18.	.5		.5	.1		8.3	(*)		.1	(*)		.1
23.	1.4	.3	.5	(*)		.4				.1		.6
27.	3.4	.3	1.3	(*)		7.7			(*)	(*)		.4
29.	.5	.1	.2			.1			(*)	(*)		.6
33.	3.5	.8	1.1	.1		(*)			(*)	.3		.6
37.	25.1	2.2	1.1	(*)		.1	(*)		.2	.3		.6
40.	1.8	3.9	.2	(*)		.1	(*)		.1	1.9		.6
44.	2.4	.4	.4	.1		.2	(*)		.2	1.2		.6
48.	.7	.3	1.5	(*)		(*)	(*)		(*)	.3		.5
52.	1.4	.8	4.4	(*)		(*)	(*)		(*)	.3		.4
56.	(*)	.6	.8	(*)		(*)	(*)		(*)	.4		.5
59.	(*)	.7	2.9	1.6		(*)	130.1			1.3	(*)	.4
E. Cruise TO-60-2 (STEP-1): September to December, 1960												
1.	.9		1.4	.7	(*)	.2	.2		.2	.2		1.2
2.	7.1	1.1	1.1	1.2		.4	.4		.1	.7		.8
3.	5.7	.4	.6	.8	(*)	.1	1.2		.5	.5		.9
4.	9.6	.3	.2	.4	(*)	.1	(*)		.3	.5		1.1
6.	5.6	5.0	.3	1.4		29.0	1.5		1.6	.4		.7
9.	3.7	.2	.1	5.3	(*)	3.0	.1		.2	.1		.7
11.	4.3		.6	1.5		.6			.1	.1		.4
17.	1.6		.3			.3	.4		1.0			.3
19.	2.3		.9	.5		.1			.3	(*)		.4
23.	4.3		1.9	.9		.8	1.6		.2	(*)		.4
27.	1.0		.3	.1		8.2	(*)		(*)	(*)		.6
30.	.8		.7	.7		3.8	(*)		.1			.4
32.	1.2		.2	.1		.1			.1			.1
35.	.3	.1	(*)	(*)		.5			.1			.9
38.	.5		.1			3.5			(*)	(*)		.4
42.	1.6	.2	.1	.3		.1			(*)	(*)		.1
45.	5.7		.2	.2	(*)	.4			(*)	(*)		.7
50.	1.6		.8	1.4		1.1	.5		.2	(*)		.5
55.	.7		1.1	.2		11.9	.5		.1			.3
59.	1.8		.6	.3		.8	.1		.1			.4
64.	1.0	.2	(*)			(*)			(*)	(*)		.1
69.	1.0	.2	.2			.2			.2	(*)		.7
73.	4.5	(*)	.4			(*)			(*)	(*)		.2
77.	5.7		.2			.3			.2	(*)		(*)
85.	1.6	3.2	.3		(*)	.5			(*)	.2		.1
F. Cruise TO-61-1: March to April, 1961												
2.	3.9	1.3	.1	.5		.1	(*)	.9		.4	.1	.6
5.	3.9	2.1	4.2	2.9		1.6	.1	.6	.3	.5	.1	1.2
14.	2.8	5.8	.4	1.3	(*)	.5	.1	.3	.1	.6	1.0	.9
16.	4.4	2.1	.2	.2	(*)	.1	(*)			.5	31.0	.4
18.	3.4	3.4	.2	1.7	(*)	.4	(*)		(*)	.7	2.1	.6
22.	3.1	6.8	.1	.4		(*)	(*)	.1	.2	.6		.6
27.	1.4	1.4	.3	.1	(*)	.5	.1		2.0	.2	.1	.3
29.	.9	2.8	1.0	.3		.1	.2	1.5	.1	1.5		.6
32.	3.9	1.7	.3	.4		(*)	(*)	.9	(*)	.7		.8
36.	.8	4.6	.1	.6	(*)	(*)	(*)	.6	.2	.8		.7
38.	4.5	1.1	.9	.1		.2	(*)	.6	(*)	.2		.7
40.	.8	1.9		(*)		(*)	(*)		(*)	.2		.3

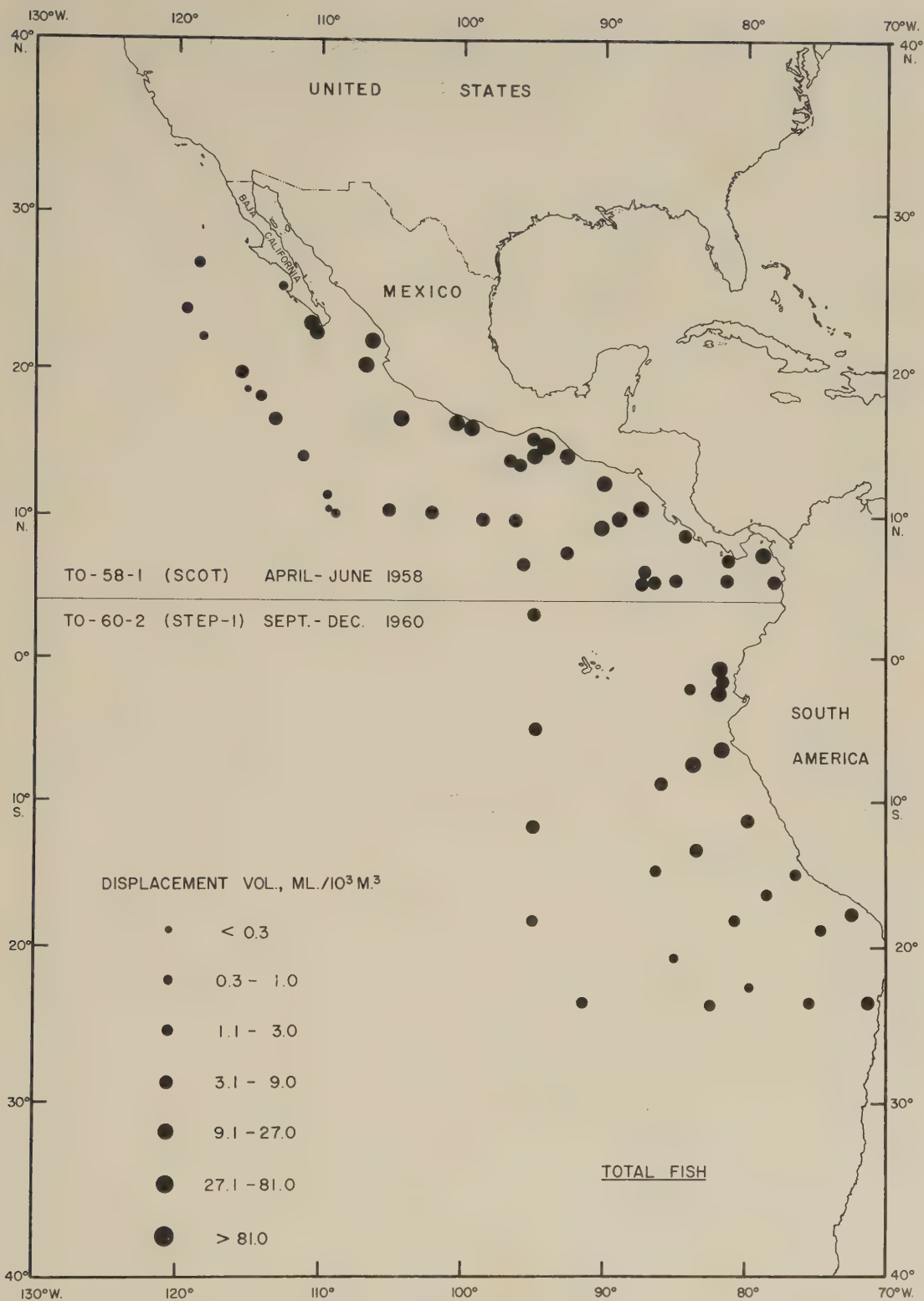


FIGURE 6.—Distribution of standing crop (standardized volume) of total fish taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

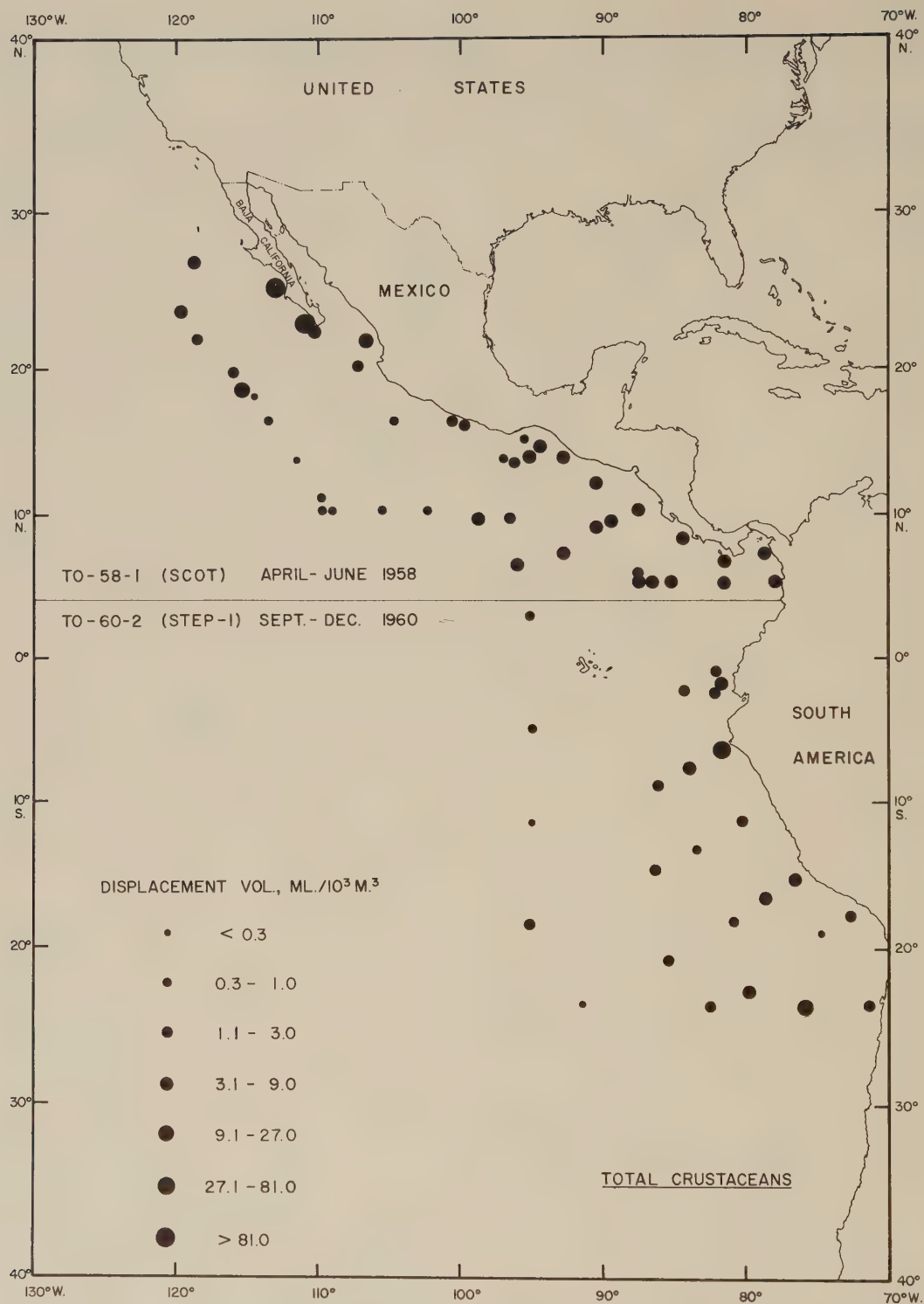


FIGURE 7.—Distribution of standing crop (standardized volume) of total crustaceans taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

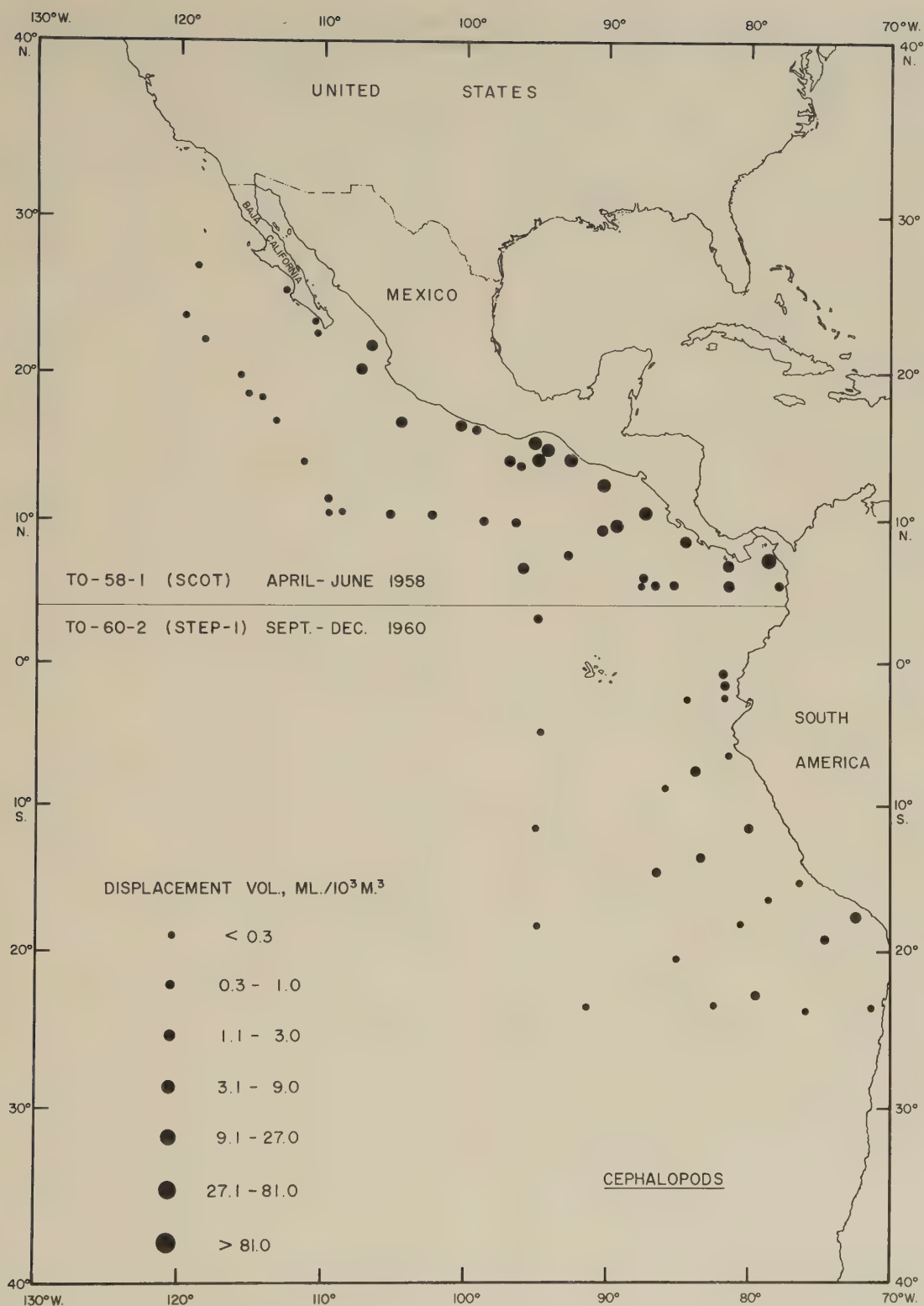


FIGURE 8.—Distribution of standing crop (standardized volume) of total cephalopods taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

TABLE 6.—Means and medians of standardized micronekton volumes (milliliters per 1,000 m.³) from stations shown in figures 1, 6, 7, and 8, grouped by distance in miles from the mainland coast

[Data from tables 1 and 5; n means number of stations]

Micronekton components	<300 miles ¹ (n=40)		300 to 600 miles ² (n=19)		>600 miles ³ (n=10)	
	Mean	Median	Mean	Median	Mean	Median
Myctophids.....	3.59	2.50	1.80	1.40	1.71	1.00
Leptocephali.....	3.30	2.20	1.00	.60	.39	.10
Gonostomatids.....	.90	.65	.52	.50	.20	.20
Total fishes.....	9.07	8.40	3.65	3.20	2.34	1.30
Euphausiids.....	1.73	.55	1.03	.30	.27	.20
Stomatopod (squillid) larvae.....	.46	.40	.10	<.10	.03	<.10
Sergestids.....	.66	.25	.31	.10	.06	<.10
Total crustaceans.....	9.22	3.60	3.67	2.00	.74	.65
Total cephalopods.....	1.67	.95	.30	.20	.15	.10
Total micronekton.....	19.96	14.00	7.62	5.10	3.23	2.35

¹ TO-58-1 stations 1, 48 to 146; TO-60-2 stations 1 to 9, 23 to 30, 42 to 50.

² TO-58-1 stations 3 to 16, 29 to 46; TO-60-2 stations 11 to 19, 32, 38, 55.

³ TO-58-1 stations 18 to 27; TO-60-2 stations 35, 59 to 85.

TABLE 7.—Means of standardized micronekton volumes from two groups of the 40 onshore stations of table 6
[Data from table 1]

Micronekton component	8 stations with total micronekton volumes each ≥ 22.0 ml./10 ³ m. ³ ¹	32 stations with total micronekton volumes each < 22.0 ml./10 ³ m. ³ ²
	ML./10 ³ m. ³	ML./10 ³ m. ³
Fishes.....	15.48	7.47
Crustaceans.....	32.26	3.46
Cephalopods.....	3.22	1.28
Total.....	50.96	12.21

¹ TO-58-1 stations 49, 63, 77, 81, 142, 144B, 146; TO-60-2 station 6.

² Stations in table 6, footnote 1, except those in footnote above.

from the eastern tropical Pacific because of the differences in sampling gear.

The distribution of leptocephali, the second largest group by volume among the fishes, is shown in figure 10. Standardized volumes are again higher near the coast than offshore (table 6), but they decline toward the south (table 5) and possibly also to the north. On a cruise made in June 1964, the mean standardized volume of leptocephali recorded at seven stations along the west coast of Baja California was < 0.1 ml. per 1,000 m.³ Leptocephali have been recorded in micronekton catches off the United States west coast and in the central Pacific, but apparently in much smaller quantities than in the coastal waters of the eastern tropical Pacific (Aron, 1959, 1962a; Percy, 1964; King and Iversen, 1962).

The distribution of gonostomatids—mainly *Vinciguerria* spp., as shown in table 3—is similar in its general features to the distribution of total fishes (fig. 6) and is, therefore, not shown. Volumes decline from onshore to offshore (table 6), and the volumes in table 5 show no obvious change with latitude for stations located at similar distances from the coast.

Similar data for two of the more common crustaceans, euphausiids and stomatopod (squillid) larvae, are given in figures 11 and 12. Euphausiids (fig. 11) are more abundant onshore than offshore (table 6) and may increase in biomass toward the poles. Figure 11 and table 5 show higher concentrations south of the Equator than elsewhere, and similar concentrations occurred on a cruise made in June 1964 along the west coast of Baja California (mean standardized volume for seven stations, 14.6 ml. per 1,000 m.³). Euphausiids are well represented in the material from Pacific regions farther north and west (Aron, 1959, 1962a; King and Iversen, 1962), although, again, the nature of the collecting gear used in those regions prevents quantitative comparisons with the eastern tropical Pacific.

The distribution of volumes of stomatopod larvae (fig. 12) is similar to that of leptocephali: higher onshore than offshore (table 6), and diminishing polewards. Figure 12 and table 5 show low concentration south of lat. 10° S., and similar concentrations occurred on a cruise made in June 1964 along the west coast of Baja California (mean standardized volume for seven stations, 0.1 ml. per 1,000 m.³). Stomatopod larvae were not mentioned by Aron (1959, 1962a) in his reports on micronekton collections west of the United States. King and Iversen (1962) obtained them fairly regularly in central Pacific waters between about lat. 19° S. (the southern limit of their sampling) and lat. 35° N.; they were not taken north of lat. 35° N.

The distribution of sergestids is similar in its general features to the distribution of stomatopod larvae and is, therefore, not shown. Volumes decline from onshore to offshore (table 6), and from the tropics toward the poles; all volumes ≥ 1.0 ml. per 1,000 m.³ in table 5 are from stations located between lat. 15° N. and 15° S.

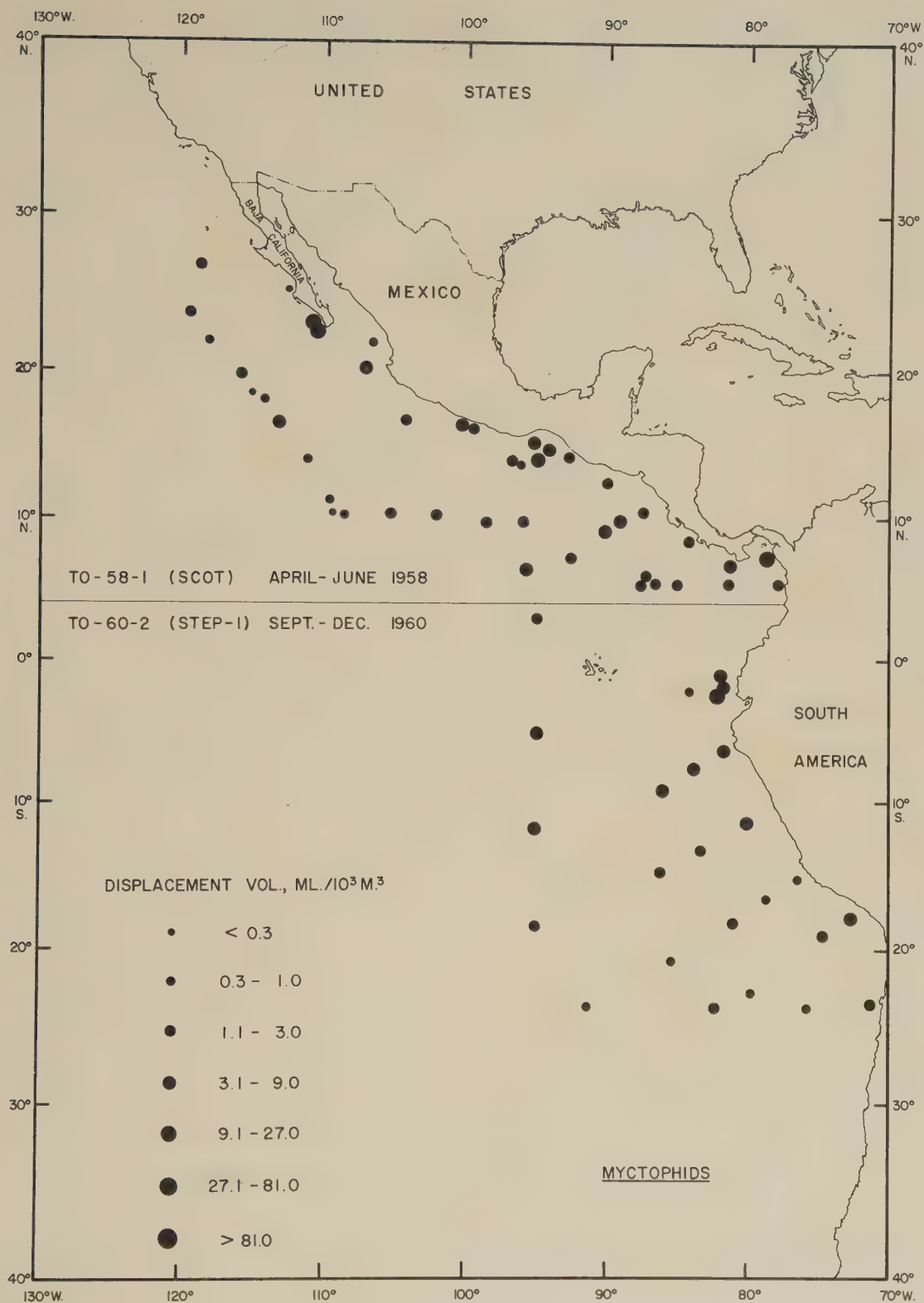


FIGURE 9.—Distribution of standing crop (standardized volume) of myctophids taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

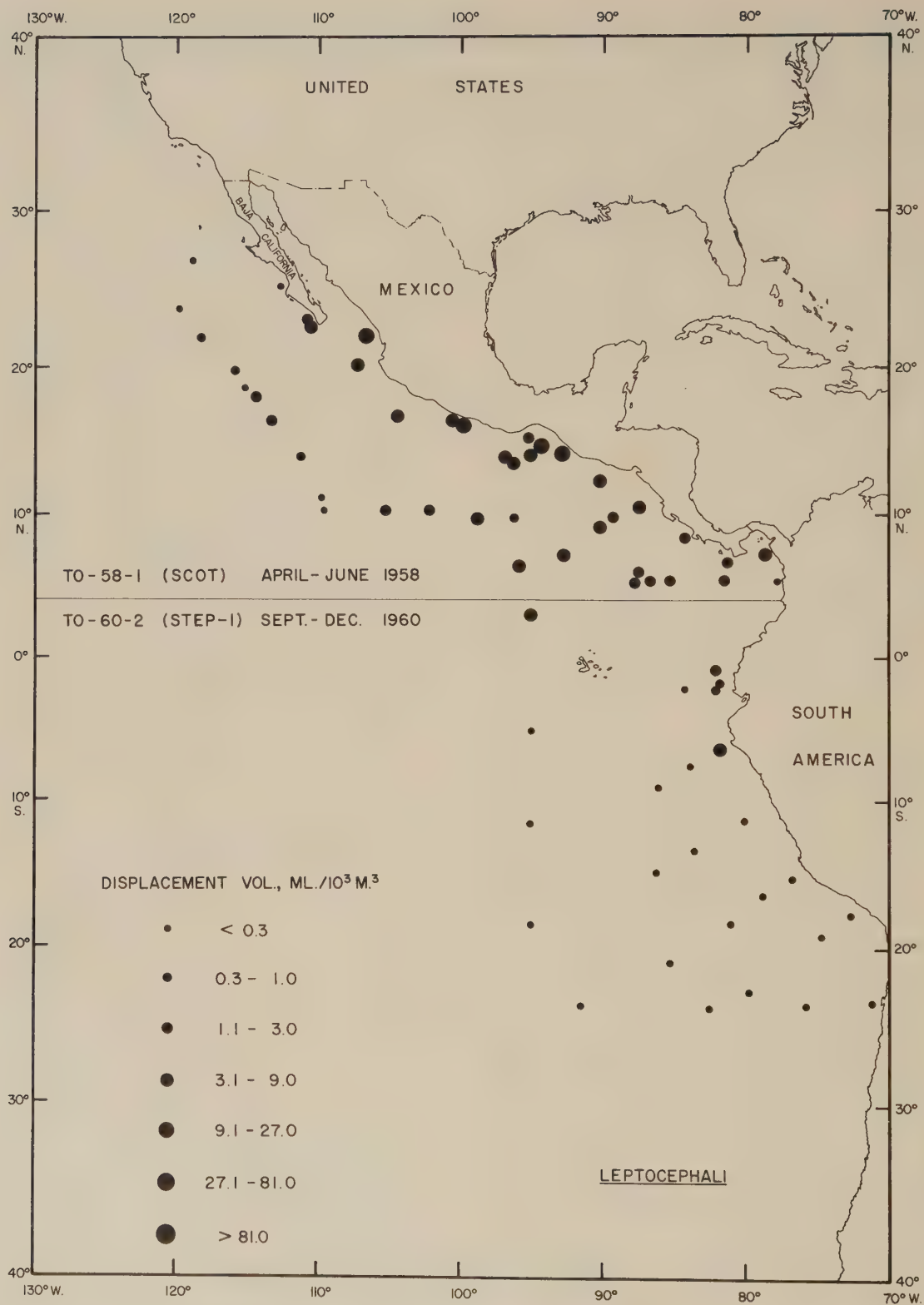


FIGURE 10.—Distribution of standing crop (standardized volume) of leptocephali taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

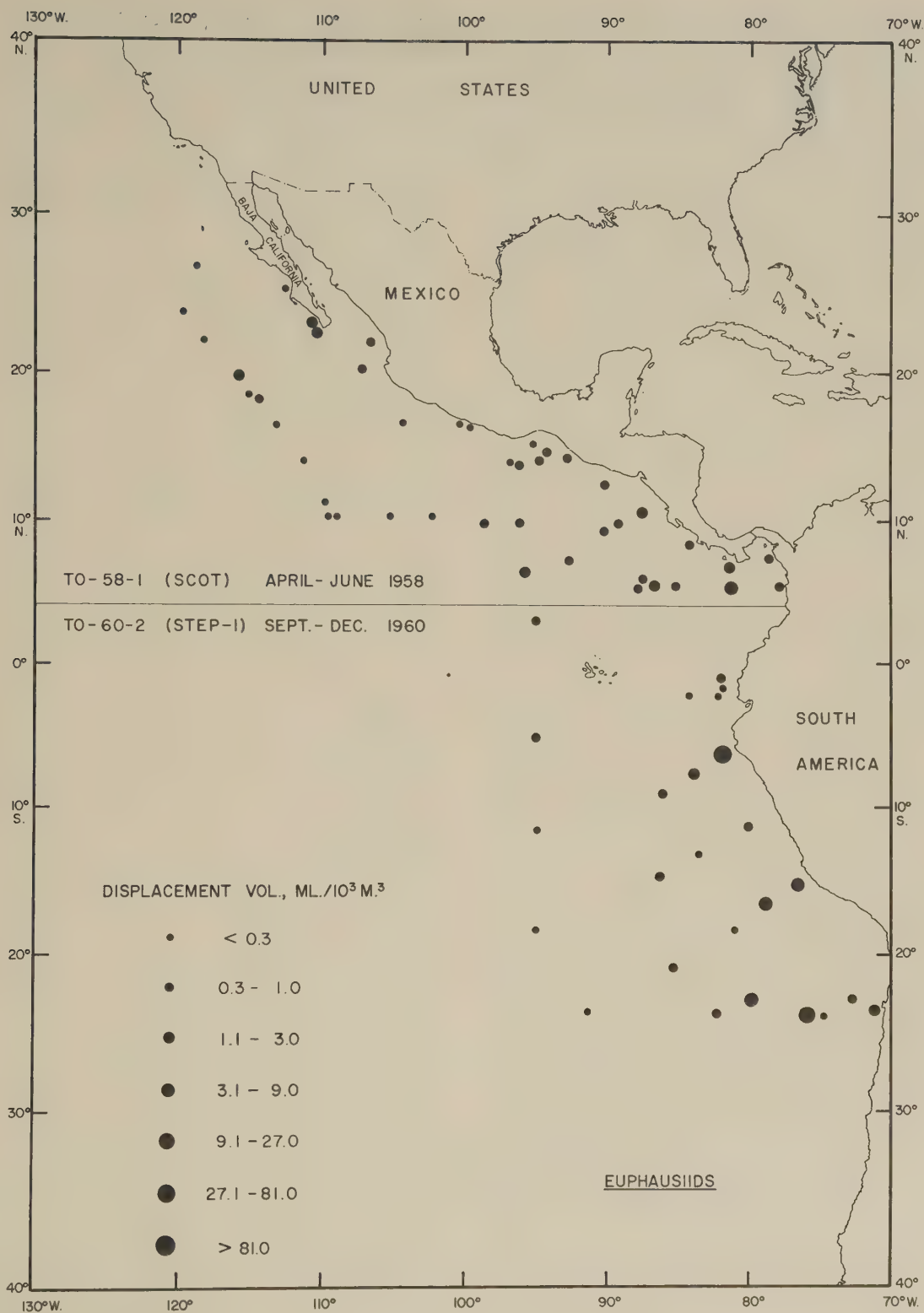


FIGURE 11.—Distribution of standing crop (standardized volume) of euphausiids taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

Figure 13 gives similar data for three other important crustacean components of the micronekton, namely galatheids, portunids, and adult stomatopods (squillids). These forms were not taken during cruise TO-60-2 and occurred at only 17 stations on cruise TO-58-1, generally only one kind to a station (although both portunids and stomatopods were collected at station 96, in a 4:1 ratio by volume, see table 5). Their distribution is much more localized than the distribution of the other components previously discussed.

The galatheids were all adult *Pleuroncodes planipes* ("red crab"); a few small samples of galatheid juveniles, which could not be identified to species, are listed in tables 3 and 5 but are not shown in figure 13. This family was by far the largest in volume for the total micronekton of all the cruises (tables 3 and 4), but it was taken only in a small part of the region covered, where it was generally very abundant. The area of occurrence shown in figure 13 (and in fig. 15, which gives data for other cruises) is the west coast of Baja California and offshore in the California Current Extension as far west as long. 120° W. and as far south as lat. 18°30' N. (Clarion Island); table 5 gives the data on which figures 13 and 15 are based. These western and southern limits are approximately the same as reported by Alverson (1963a) and Longhurst (1967); according to these authors, *P. planipes* also occurs farther east (across the Gulf of California) and farther north (to Monterey in central California). It did not occur in the material of Aron (1959, 1962a) or King and Iversen (1962). Because of the generally high standing crops of this animal encountered in area 1, this area yielded 47.4 percent of all the total micronekton collected in the 18 areas (table 3), although only 21 hauls (16.0 percent of the total for all areas) were made there (table 1); mean standardized volume of *P. planipes* for the hauls was 56.9 ml. per 1,000 m.³ (table 5). Area 1 includes several localities where coastal upwelling occurs seasonally, as noted earlier.

The portunid material of figures 13 and 15 was 99.4 percent *Portunus affinis* (table 3). Portunids were taken in the 1.5-m. net only along the coast from southeastern Mexico to northern Colombia,

to about 200 nautical miles (370 km.) offshore. Alverson (1963a) charted a distribution of *P. affinis* which has a greater range in latitude (about 23° N. to 10° S.) and a wider range offshore (to about 700 nautical miles—1,300 km.—from the continent). Aron (1959, 1962a) did not mention portunids; King and Iversen (1962) recorded only two individuals from the central Pacific, both from tropical latitudes.

The stomatopod adults (or near-adults—our specimens were pelagic, whereas adults are generally regarded as benthic) were even more localized than the galatheids and portunids. They were taken only along the coast of southeastern Mexico, especially in the Gulf of Tehuantepec (figs. 13 and 15). Alverson (1963a) noted that they occurred in tuna stomachs only in areas 4 and 5, which include the Gulf of Tehuantepec. Their abundance in that region may be associated in some way with the fact that the Continental Shelf is wider in the eastern part of the Gulf of Tehuantepec and in the western part of area 5 than it is along most parts of the eastern side of the eastern tropical Pacific.

Figures 14 to 16 give information for total fish, crustacean, and cephalopod micronekton taken in night hauls on four other cruises (TO-59-1, TO-59-2, TO-60-1, and TO-61-1), which were made only along the Pacific coasts of Mexico and Guatemala; to the extent that cruise TO-58-1 was concerned with that area, the information about it (the same as in figs. 6 to 8) has been included to facilitate comparison between seasons (see below). Figure 2 identifies the stations (see also table 1).

The main features of distribution by area which these figures show have already been mentioned. In figure 15, code letters indicate the kind of crustaceans which accounted for half or more of the volume of Crustacea at a particular station. Included were penaeids at station 59 of cruise TO-60-1, which contributed practically all the material of this family for all the cruises, as well as the groups listed above. Many of the stations had a heterogeneous crustacean fauna, of which no one group made up half or more of the volume (table 5); the number of these stations increased toward the tropics.

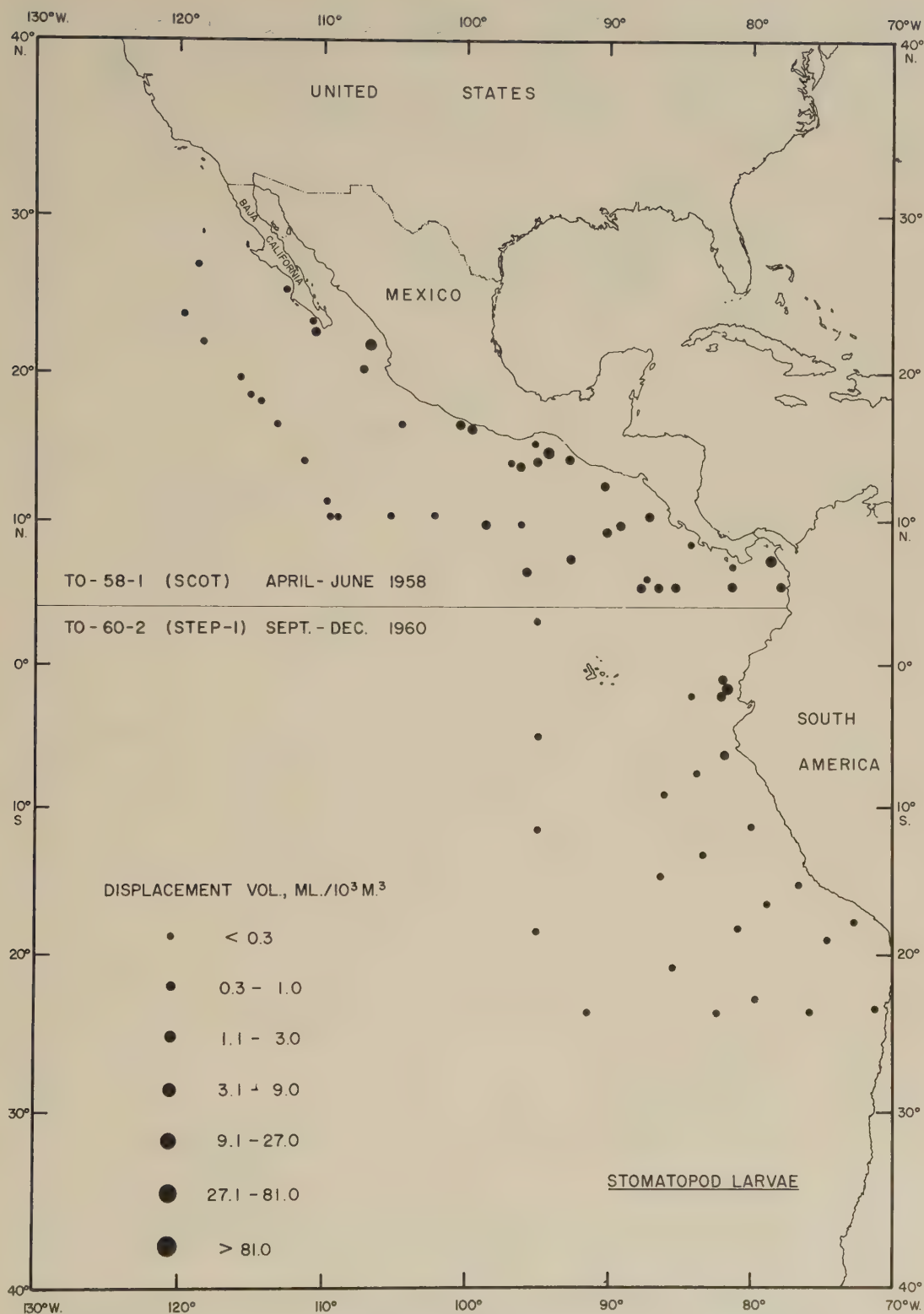


FIGURE 12.—Distribution of standing crop (standardized volume) of stomatopod (squillid) larvae taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

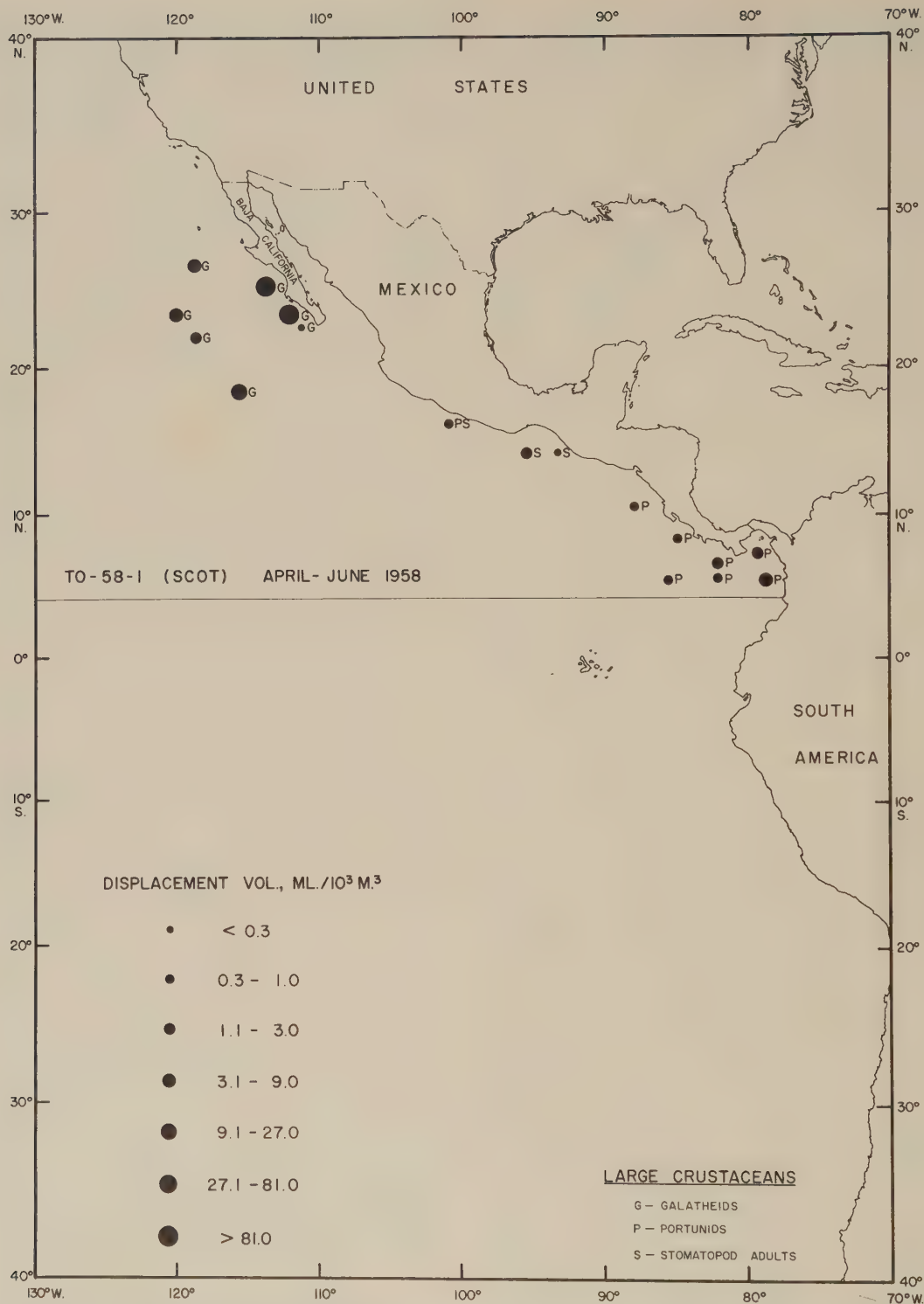


FIGURE 13.—Distribution of standing crop (standardized volume) of large crustaceans, namely galatheids, portunids, and adult stomatopods (squillids), taken in night micronekton hauls on cruises TO-58-1 and TO-60-2.

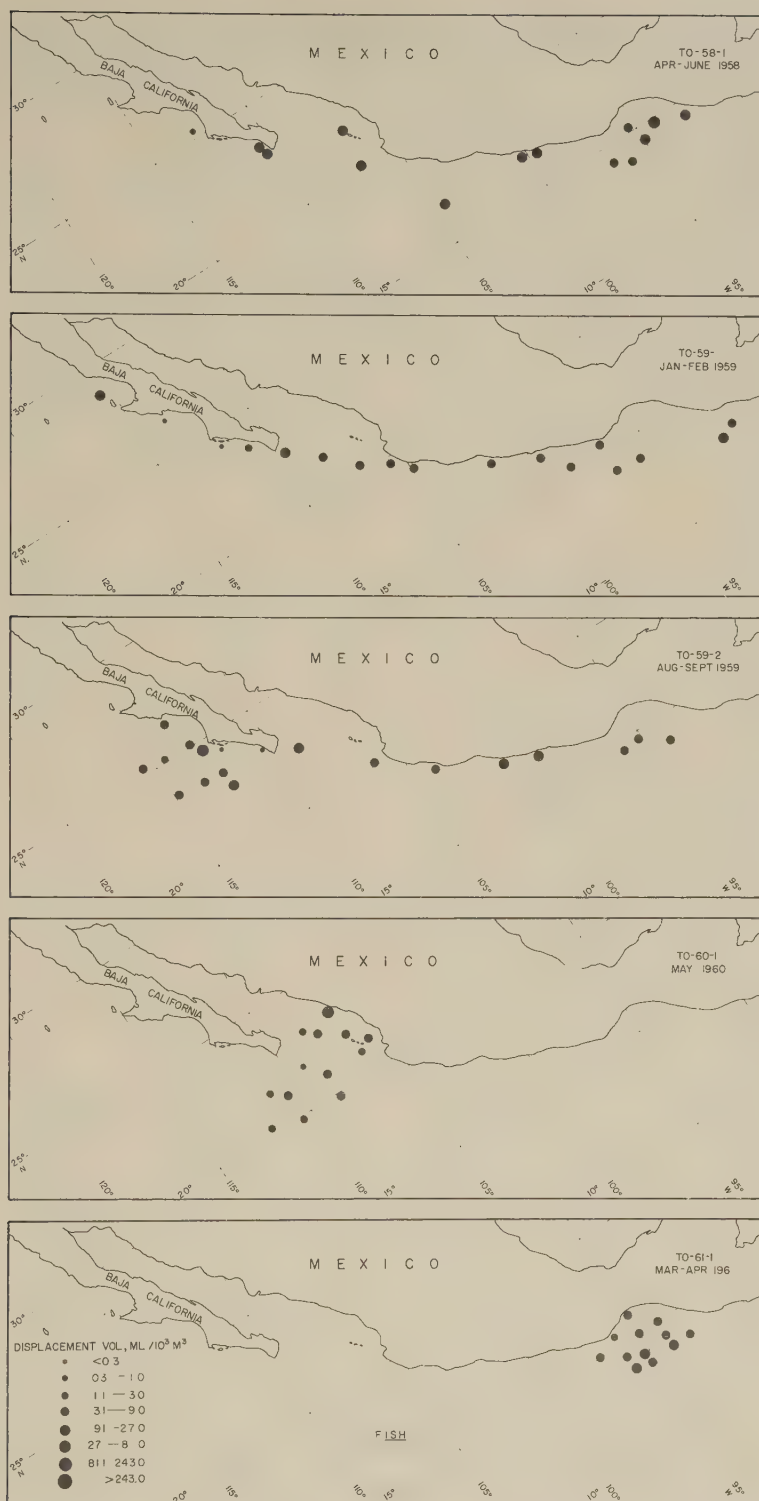


FIGURE 14.—Distribution of standing crop (standardized volume) of total fish taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala.

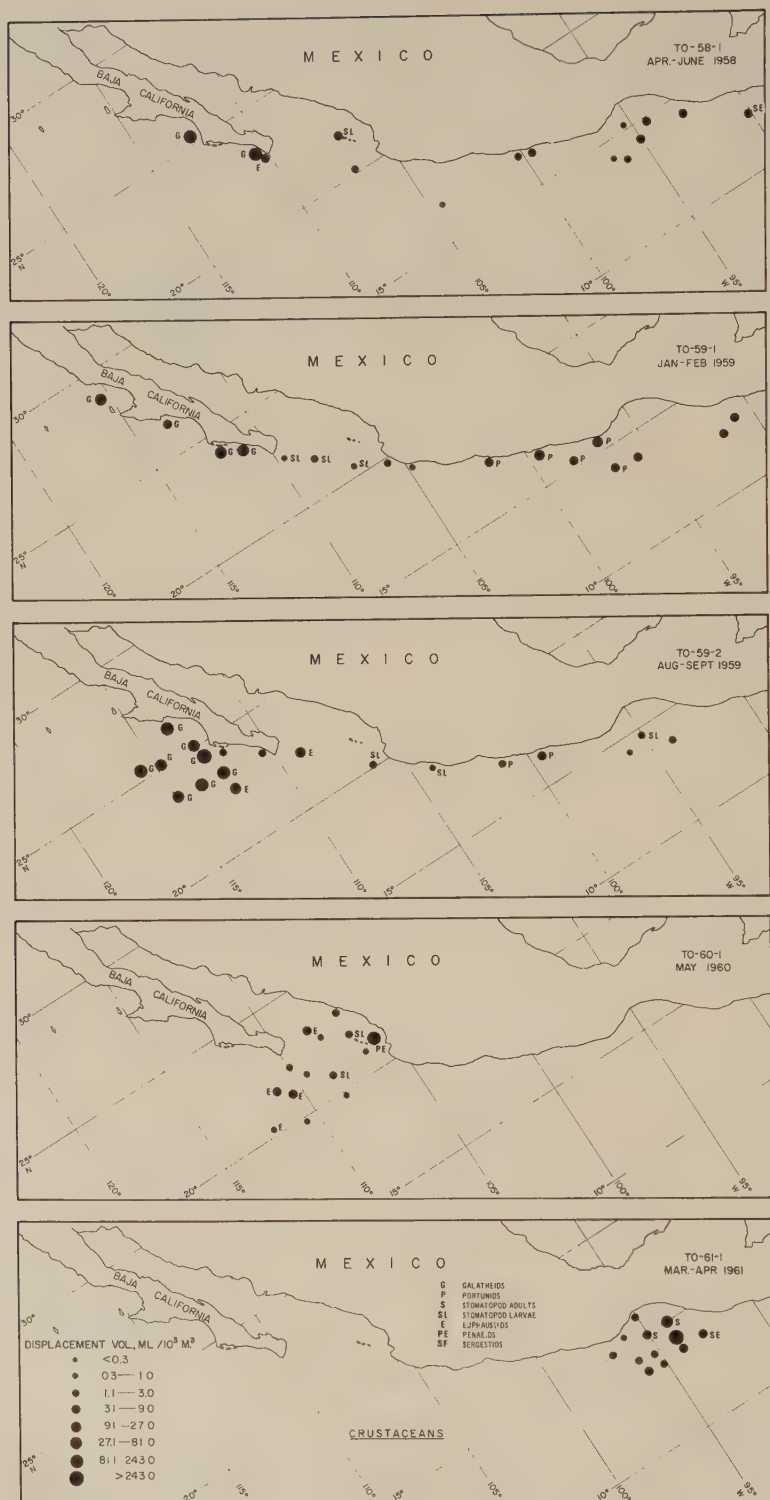


FIGURE 15.—Distribution of standing crop (standardized volume) of total crustaceans taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala. Code letters, explained in the bottom panel, indicate the group, if any, which represented half or more by volume of the catch of crustaceans.

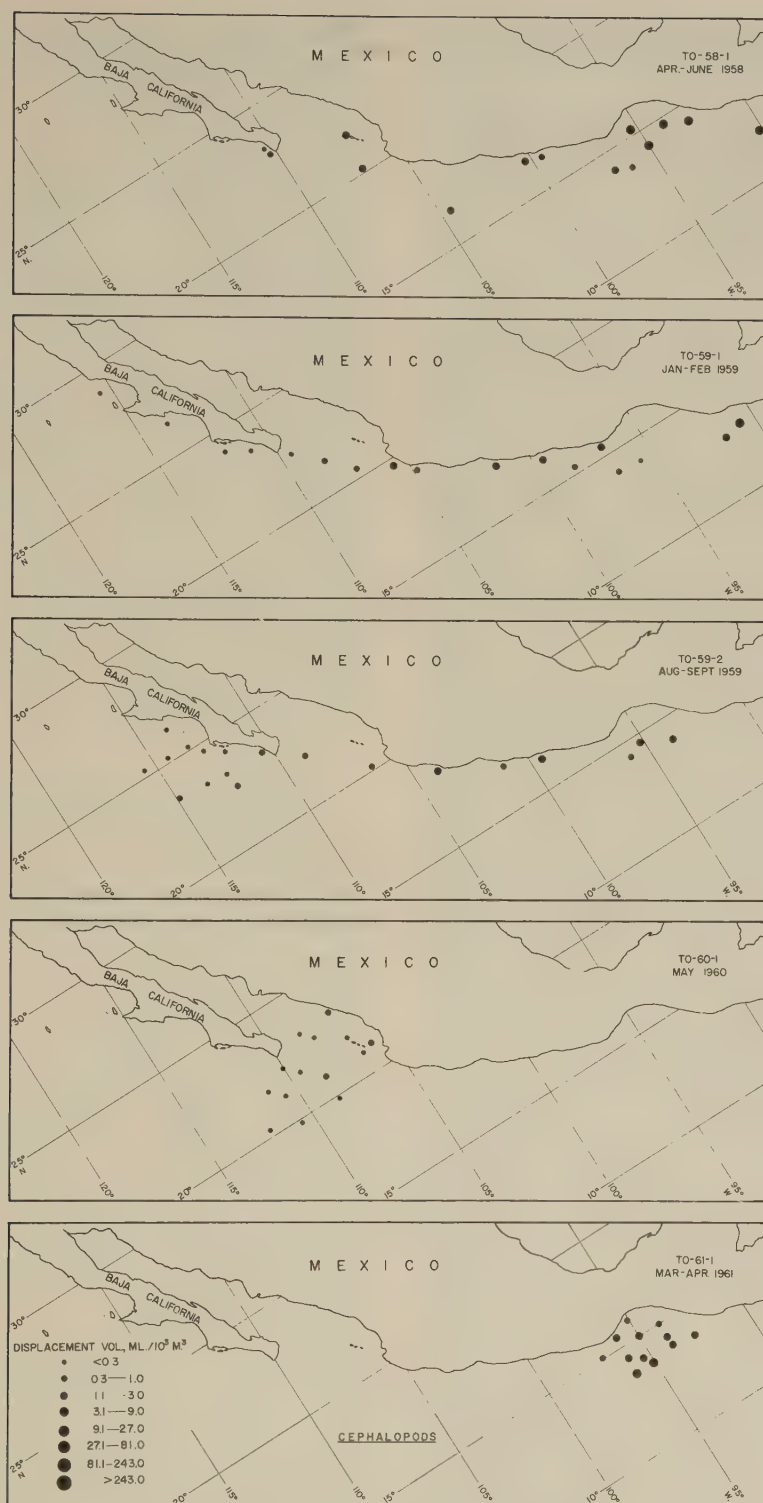


FIGURE 16.—Distribution of standing crop (standardized volume) of total cephalopods taken in night micronekton hauls on cruises made along the Pacific coasts of Mexico and Guatemala.

DISTRIBUTION OF MICRONEKTON BY SEASONS

The only series of cruises which could possibly reveal seasonal changes in the micronekton of standard night hauls is the series for the Pacific coasts of Mexico and Guatemala—cruise TO-58-1 in part, and cruises TO-59-1, TO-59-2, TO-60-1, and TO-61-1—for which results are summarized in figures 14 to 16.

Except for TO-60-1, these cruises were planned to determine certain seasonal changes in the standing crop of micronekton, and other ocean properties, in the Gulf of Tehuantepec (long. 95° W.). Comparisons for this area are available for the months January–February (TO-59-1; no data for the center of the Gulf, because of bad weather), March–April (TO-61-1), May–June (TO-58-1), and August–September (TO-59-2). The data in figures 14 to 16 show that all three main components of the micronekton were scarcer by volume in this area in August–September than in March–June (possibly January–June). This difference is to be expected from the study by Blackburn (1962, 1963) of seasonal changes in the physical, chemical, and biological oceanography of the Gulf. The physical processes that cause shoaling of the pycnocline in certain areas and intermittent vertical mixing in parts of these areas are well developed in winter, and nutrient-rich water brought to the surface could be expected to result in a high crop of micronekton by spring. On the other hand, the eutrophic conditions decline through the spring, and the micronekton crop of late summer should be low. The time required for a crop of micronekton to grow has been discussed by Blackburn (1966a).

Off the west coast of Baja California, eutrophic conditions (coastal upwelling) are generally most pronounced in spring (Reid et al., 1958). If a lag of a few months is assumed between the appearance of a physical eutrophic process and the appearance of the resulting crop of micronekton (see previous paragraph), an increase in micronekton volume from winter through spring to late summer might be expected. The data for fish and cephalopods (figs. 14 and 16) are not inconsistent with this hypothesis, but they are generally scanty (except for August–September). For crustaceans (mainly *Pleuroncodes planipes*) the data in figure 15 suggest a rather high abundance throughout the

whole period mentioned above. Longhurst (1967), who analyzed occurrences of *P. planipes* in zooplankton net hauls, drew a similar conclusion. Practically no quantitative data are yet available from micronekton hauls on occurrences of *P. planipes* in October through December, although it was abundant in hauls made with the high-speed net in December 1960. Data on *P. planipes* from zooplankton net hauls also are scanty at this period, and it is possible that the species is then less abundant than during the rest of the year, although the evidence is inconclusive (Longhurst, 1967). The distribution and ecology of this animal are being further studied in the Scripps Tuna Oceanography Research Program.

Elsewhere along the Mexican coast, namely across the mouth of the Gulf of California and thence southwards along the coast to the Gulf of Tehuantepec, no hypothesis about seasonal distribution of micronekton has been developed to test, and the scanty data in figures 14 to 16 do not suggest any particular seasonal change.

COMPARISON OF MICRONEKTON CAUGHT BY NETS AND TUNAS

Alverson (1963a), who sorted stomach contents of 2,846 yellowfin tuna⁵ and 1,010 skipjack tuna⁵ from the eastern tropical Pacific, published tables showing the percentage composition by volume of this material by taxa (including some species) for each of the areas 1 to 14 of figure 5.

Alverson's specimens of tuna were obtained from commercial catches made by surface hooking (bait-and-pole) or surface netting (purse seine). Yellowfin tuna are caught also by subsurface hooking (pelagic long-line) in parts of the eastern tropical Pacific, but few data on stomach contents are available for fish from that region (Juhl, 1955; Blunt, 1960).

Tables 8 to 14 compare the percentage composition of actual volumes of micronekton from standard night hauls with the actual volumes of stomach contents of yellowfin and skipjack tuna, for areas in which at least five hauls were available (namely areas 1, 2, 3, 4, 5, 6, and areas 11 and 12

⁵ These two species of tuna were called, respectively, *Neothunnus macropterus* and *Katsuwonus pelamis*, by Alverson; according to Collette and Gibbs (1963), they should be known as *Thunnus albacares* (Bonnaterre) and *Euthynnus pelamis* (Linnaeus).

combined). The source of data for the net hauls is table 3 of this paper; the sources for the tuna stomach contents are various tables by Alverson (1963a).

Each of the tables 8 to 14 shows the percentage composition of fish, crustaceans, and cephalopods in material caught by the 1.5-m. net, by yellowfin tuna, and by skipjack tuna, respectively, for a particular area. Each of the three main categories is then further divided into components (generally families), of which each accounted for at least 0.5 percent by volume of the total material (from 1.5-m. net, yellowfin tuna, or skipjack tuna), for the area; other components (including material not identified to family) were lumped. The percentages in tables 12 and 14 for skipjack tuna differ slightly from the corresponding percentages in Alverson's tables, because he included small amounts of materials from stomachs of skipjack tuna (1.5 percent in area 5; 0.3 percent in areas 11 and 12) which are not regarded as micronekton. Alverson separated Thunnidae from Katsuwonidae in the fish families represented in his material, but they are here combined as Thunnidae, and have been so entered in table 3 and tables 8 to 14. Volumes for groups of animals in tables 8 to 14 include all ontogenetic stages unless otherwise stated.

TABLE 8.—Percentage taxonomic composition of micronekton in area 1 of figure 5, from net hauls and tuna stomachs

[21 standard night net hauls of 1.5-m. net (18,971 ml.); 567 stomachs of yellowfin tuna (37,489 ml.); 151 stomachs of skipjack tuna (4,661 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Myctophidae.....	7.1		
Leptocephali.....	.5		
Gonostomatidae (<i>Vinciguerria</i>).....	.7		
Engraulidae.....		9.6	28.3
Scomberesocidae.....			9.5
Scombridae.....		2.0	
Other fish.....	.1	7.8	5.6
Total fish.....	8.4	19.4	43.4
Galatheididae.....	81.5	78.1	36.8
Euphausiidae.....	8.1		19.2
Pisiphaeidae.....	1.5		
Other crustaceans.....	.3	.3	(*)
Total crustaceans.....	91.4	78.4	56.0
Cephalopods.....	.2	2.2	.6
Grand total.....	100.0	100.0	100.0

TABLE 9.—Percentage taxonomic composition of micronekton in area 2 of figure 5, from net hauls and tuna stomachs

[6 standard night net hauls of 1.5-m. net (827 ml.); 328 stomachs of yellowfin tuna (62,225 ml.); 48 stomachs of skipjack tuna (1,862 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Myctophidae.....	16.2		
Leptocephali.....	9.4		
Gonostomatidae (<i>Vinciguerria</i>).....	7.5	(*)	5.3
Gonostomatidae (others).....	.8		
Ostracidae.....	(*)	21.1	.5
Thunnidae.....		19.9	
Tetraodontidae.....		15.6	
Serranidae.....		4.7	5.0
Exocoetidae.....		1.9	
Ballistidae.....		.6	
Carangidae.....		.5	
Other fish.....	.8	3.7	10.1
Total fish.....	34.7	68.0	20.9
Galatheididae.....	56.8	31.1	78.3
Euphausiidae.....	4.6	(*)	.1
Squillidae (larvae).....	1.0	(*)	(*)
Other crustaceans.....	1.8	.1	.2
Total crustaceans.....	64.2	31.2	78.6
Enoploteuthidae.....	.9		
Other cephalopods.....	.2	.8	.5
Total cephalopods.....	1.1	.8	.5
Grand total.....	100.0	100.0	100.0

TABLE 10.—Percentage taxonomic composition of micronekton in area 3 of figure 5, from net hauls and tuna stomachs

[18 standard night net hauls of 1.5-m. net (3,836 ml.); 155 stomachs of yellowfin tuna (12,062 ml.); 5 stomachs of skipjack tuna (247 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Leptocephali.....	17.0		
Myctophidae.....	13.6	0.1	
Gonostomatidae (<i>Vinciguerria</i>).....	7.0	.5	27.2
Gonostomatidae (others).....	.7		
Bregmacerotidae.....	1.3	(*)	
Stomatidae.....	.5		
Thunnidae.....	(*)	12.2	23.9
Coryphaenidae.....	(*)	7.0	
Polynemidae.....		1.6	34.1
Carangidae.....		1.5	
Ballistidae.....		.7	
Exocoetidae.....	.2	.6	
Other fish.....	1.1	10.9	14.0
Total fish.....	41.4	35.1	99.2
Penaeidae.....	39.8		
Euphausiidae.....	6.9		
Squillidae (larvae).....	4.3	.7	.8
Galatheididae.....	(*)	41.0	
Other crustaceans.....	2.7	.2	
Total crustaceans.....	53.7	41.9	.8
Enoploteuthidae.....	3.3		
Cranchiidae.....	1.5		
Onychoteuthidae.....		4.7	
Other cephalopods.....	.1	18.3	(*)
Total cephalopods.....	4.9	23.0	(*)
Grand total.....	100.0	100.0	100.0

TABLE 11.—Percentage taxonomic composition of micronekton in area 4 of figure 5, from net hauls and tuna stomachs

[29 standard night net hauls of 1.5-m. net (7,191 ml.); 247 stomachs of yellowfin tuna (14,839 ml.); 1 stomach of skipjack tuna (97 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Leptocephali	28.3		
Myctophidae	21.7	1.8	
Gonostomatidae (<i>Vinciguerria</i>)	4.5	(*)	
Idiacanthidae	.8		
Heterosomata	.6		
Stomiidae	.6		
Bregmacerotidae	.5		
Thunnidae	(*)	10.8	
Carangidae	(*)	10.4	
Exocoetidae		8.8	93.8
Balistidae		.8	
Other fish	2.2	8.0	6.2
Total fish	59.2	40.6	100.0
Portunidae	11.6	40.6	
Squillidae (adults)	6.6	13.5	
Squillidae (larvae)	3.2	.3	
Euphausiidae	1.3		
Sergestidae	1.3		
Unid. crab megalopa	.5		
Galatheididae	.2	1.0	
Other crustaceans	3.6		
Total crustaceans	28.3	55.4	
Enoploteuthidae	6.7		
Cranchiidae	5.1		
Ommastrephidae		.7	
Other cephalopods	.7	3.3	
Total cephalopods	12.5	4.0	
Grand total	100.0	100.0	100.0

Differences between micronekton from nets and tuna stomachs were rather marked as far as percentages of fish families are concerned. Myctophidae was the largest fish component of net material in most areas, but in tuna stomachs it was generally a small component, where it occurred at all. Only in area 5 (yellowfin tuna) and possibly area 6 (skipjack tuna) were the percentages for tuna comparable with those for nets. Leptocephali, a large item in net catches in most areas, were represented in tuna stomachs only as a negligible percentage in area 6 (yellowfin tuna). The occurrence of the gonostomatid fish *Vinciguerria* (which is shown separately from other members of the family because it is the only one recorded from tuna stomachs) was reasonably similar in the three kinds of material in tables 8 to 14 considered as a whole. Sternoptychidae, Bregmacerotidae, Nemichthyidae, Stomiidae, Idiacanthidae, and Bathylagidae were significant components of net micronekton in some areas, but never of tuna stomach contents (unless they occurred in the unidentifiable fish remains, which have been included

TABLE 12.—Percentage taxonomic composition of micronekton in area 5 of figure 5, from net hauls and tuna stomachs

[10 standard night net hauls of 1.5-m. net (2,470 ml.); 319 stomachs of yellowfin tuna (16,256 ml.); 42 stomachs of skipjack tuna (661 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Leptocephali	22.6		
Myctophidae	16.3	21.6	
Gonostomatidae (<i>Vinciguerria</i>)	3.4	.7	
Nemichthyidae	2.4		
Stomiidae	1.9		
Idiacanthidae	1.9		
Bathylagidae	1.6		
Heterosomata	1.1	(*)	
Stromateidae	.9		
Exocoetidae		17.4	
Thunnidae	(*)	1.5	
Balistidae		.8	0.7
Sternoptychidae	(*)		1.0
Other fish	2.3	11.8	61.4
Total fish	54.4	53.8	63.1
Sergestidae	7.5		
Squillidae (larvae)	4.4	2.2	7.1
Euphausiidae	4.1	(*)	(*)
Portunidae	1.7	27.2	2.7
Penaeidae	1.2		
Phronimidae	1.0		
Squillidae (adults)	.6	1.1	
Oxycephalidae	.5		
Unid. crab megalopa	.3	.3	12.4
Galatheididae	(*)	1.8	
Other crustaceans	3.5	.2	.6
Total crustaceans	24.8	32.8	22.8
Enoploteuthidae	13.0		
Cranchiidae	4.1		
Argonautidae	(*)	.9	3.7
Other cephalopods	3.7	12.5	10.4
Total cephalopods	20.8	13.4	14.1
Grand total	100.0	100.0	100.0

in "other fish"). Most of the families mentioned in this paragraph are generally regarded as mesopelagic.

On the other hand, some significant fish components of tuna stomach contents were absent or scarce in net catches—Engraulidae, Scombridae, Scomberesocidae, Ostracidae, Tetraodontidae, Thunnidae, Serranidae, Exocoetidae, Coryphaenidae, Polynemidae, Carangidae, Gadidae, and Trichiuridae. These families are generally regarded as epipelagic. Engraulidae occurred in tuna stomachs only in area 1, and their absence in net catches for that area may reflect the fact that they occur mainly in the northern half of the area, whereas the net hauls were made principally in the southern half; the 1.5-m. net has some capacity for catching engraulids, because a specimen of *Engraulis mordax* was caught in area 1 in June 1964, after the tables in this paper were compiled. The absence or scarcity of Ostracidae, Tetraodontidae, Serranidae, Gadidae, and Trichiuridae in

TABLE 13.—Percentage taxonomic composition of micronekton in area 6 of figure 5, from net hauls and tuna stomachs

[5 standard night net hauls of 1.5-m. net (1,365 ml.); 204 stomachs of yellowfin tuna (15,698 ml.); 517 stomachs of skipjack tuna (26,583 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Myctophidae	33.2	1.4	5.7
Leptocephali	7.0	(*)	
Sternopterychiidae	3.4		(*)
Gonostomatidae (<i>Vinciguerria</i>)	2.4	4.7	13.4
Nemichthyidae	1.5	(*)	
Bathylagidae	1.0		
Stomiidae	.7		
Scopelarchidae	.5		
Scombridae		25.0	
Thunnidae		16.0	
Gadidae	.1	.7	.3
Exocoetidae		.7	4.9
Carangidae	.1	3.2	.2
Trichiuridae	.4	1.2	6.4
Other fish	1.3	20.1	4.1
Total fish	51.6	77.0	35.0
Euphausiidae	32.0	(*)	59.9
Penaeidae	3.7		
Sergestidae	2.9		
Squillidae (larvae)	2.3	.4	.2
Portunidae		10.2	
Other crustaceans	4.0	.5	.7
Total crustaceans	44.9	11.1	60.8
Enoploteuthidae	2.0		1.6
Cranchiidae	1.0		.2
Ommastrephidae		1.4	
Other cephalopods	.5	10.5	2.4
Total cephalopods	3.5	11.9	4.2
Grand total	100.0	100.0	100.0

net catches, in areas where they were significant in tuna stomachs, may reflect the fact that only five or six net hauls were made in each of those areas. The other major differences in representation of families in net catches and tuna stomach contents probably indicate real differences between the catching performance of the net and of the tunas, discussed below. Carangidae are possibly underrepresented in the net material of area 4; some hauls taken in that area on cruise TO-62-1, which are neglected in most parts of this paper for reasons given elsewhere, were moderately rich in carangids (table 2).

A similar situation is suggested by the cephalopod data of tables 8 to 14, which show the main families in net catches little represented in tuna stomachs and vice versa; but the component "other cephalopods" (which is mainly material that was too much digested for identification) was relatively large in the tuna stomach contents, and the principal components of the net catches (Enoploteuthidae and Cranchiidae) might have occurred in it.

TABLE 14.—Percentage taxonomic composition of micronekton in areas 11 and 12 of figure 5, from net hauls and tuna stomachs

[6 standard night net hauls of 1.5-m. net (1,138 ml.); 72 stomachs of yellowfin tuna (4,880 ml.); 37 stomachs of skipjack tuna (2,321 ml.); asterisk means <0.05 percent]

Group of animals	Source of material		
	1.5-m. net	Yellowfin tuna	Skipjack tuna
	Percent	Percent	Percent
Myctophidae	19.8	1.0	
Leptocephali	17.5		
Idiacanthidae	3.0		
Stomiidae	2.7		
Gonostomatidae (<i>Vinciguerria</i>)	2.5	(*)	
Bregmacerotidae	1.6		
Carangidae		9.8	2.8
Exocoetidae		1.5	89.8
Paralepididae	(*)	.5	
Other fish	1.4	6.6	6.8
Total fish	48.5	19.4	99.4
Euphausiidae	14.3	.1	
Sergestidae	12.1	1.4	
Portunidae	5.7	71.7	(*)
Squillidae (larvae)	4.0	(*)	(*)
Phronimidae	1.1	(*)	
Penaeidae	.7		
Palinuridae	.7		
Phrosinidae	.6		
Unid. crab megalopa	.5		(*)
Other crustaceans	5.0	1.2	
Total crustaceans	44.7	74.4	0.1
Enoploteuthidae	5.1	(*)	
Cranchiidae	1.3		
Loliginidae		(*)	
Other cephalopods	.4	6.2	.5
Total cephalopods	6.8	6.2	.5
Grand total	100.0	100.0	100.0

The crustacean components were much more alike than the fish and cephalopod components, qualitatively and quantitatively, in the micronekton from nets and in the stomachs of yellowfin and skipjack tunas. The galatheids were represented by large and somewhat comparable percentages in all three series in areas 1 and 2, where the material was mostly *Pleuroncodes planipes*. Percentages of similar material were very different in area 3 (very low in net catches, high in stomachs of yellowfin tuna, nil in the scanty material from skipjack tuna), but the percentage in net catches would have been higher if a special group of hauls from the Cape San Lucas front had been included (see Griffiths, 1965). Percentages of galatheids in areas 4 and 5 were small and similar for net catches and yellowfin tuna, and this material consists mainly of juveniles. Percentages of euphausiids in net micronekton were comparable with those in stomachs of skipjack tuna in some areas (especially 1 and 6) but the percentages were uniformly very low, or nil, in yellowfin tuna. Squillid larvae occurred in net

catches and in stomachs of both tuna species in most areas in somewhat similar percentages, although those in net micronekton were generally higher than those in tuna stomachs. Adult squillids were a significant item only in areas 4 and 5. There they occurred comparably in net catches and stomachs of yellowfin tuna; the skipjack material, in which they did not occur, was scanty for those areas.

Percentages of portunids were less similar; they were generally much higher for yellowfin tuna stomachs than for net catches or skipjack tuna stomachs. Percentages of unidentified crab megalopa were variable, but generally low except in stomachs of skipjack tuna from area 5. Sergestids occurred in the net micronekton of some areas, sparsely in the yellowfin tuna stomachs of areas 11 and 12, and not at all in skipjack tuna. Other crustacean families and groups in tables 8 to 14 (Pasiphaeidae, Penaeidae, Phronimidae, Oxycephalidae, Phrosinidae, and Palinuridae) appeared in the net catches only and on the whole sparsely, in the areas to which the tables refer.

Possible reasons for the differences in percentage composition of the micronekton as caught by nets and by tunas are given in the following paragraphs. These reasons are in addition to the sparse and probably unrepresentative sampling for net micronekton and skipjack tuna stomachs in some areas, to which reference has already been made. It is also possible that tuna concentrate for feeding upon aggregations of certain species of prey; such species might, therefore, be better represented in tuna stomachs than in net catches.

(1) The nets were used at night, but most tunas from the surface-hook and surface-net fisheries are caught in the daytime. Because diurnal vertical movement causes many kinds of micronekton to be more plentiful in near-surface waters by night than by day, the nets and tunas probably sample different assemblages of micronekton. This point was discussed by King and Iversen (1962), who found some of the same differences between net-caught and tuna-caught micronekton as those described above.

(2) The nets fish through a layer of water some 90 to 95 m. thick, but the range of depth at which surface-caught yellowfin tuna and skipjack tuna feed is unknown. If, as seems likely, the tuna feed closer to the surface than the average depth of the

net, epipelagic organisms would probably be better represented in tuna stomachs than in net catches.

(3) Tuna may fail to catch organisms which are available for capture, for lack of stimuli which release feeding behavior. Such stimuli can be visual or chemical (Magnuson, 1963, and references there). Visual stimuli could be lacking in the presence of suitable prey by night, or by day if the organisms are translucent.

(4) Nets, even at a speed of 5 knots, may fail to catch certain kinds of alert or strong micronekton that could be captured by tunas, which are credited with swimming speeds up to 40 knots in short bursts (Walters and Fierstine, 1964).

(5) Tuna stomachs frequently contain a significant proportion of semidigested material which is not identifiable to family. This was so in Alverson's material. Some families of micronekton might, therefore, be eaten by tunas despite their absence in the appropriate columns of tables 8 to 14.

A combination of the first and third points (netting by night, but tuna feeding by day) could explain the much better representation of myctophids, sternoptychids, nemichthyids, stomiatids, idiacanthids (and perhaps other mesopelagic fish families mentioned above, and sergestids), in the net-caught than in the tuna-caught micronekton. These groups are known to move closer to the sea surface by night (when tunas probably cannot see them well) than by day (when they are probably too deep, generally, for the tunas to catch). Alverson (1961) showed that tunas will catch the myctophid *Benthosema pterota* when it is available at the surface in daylight. It is not clear that this explanation could apply to leptocephali, but these animals might not be taken by tunas because of their translucence; the same might apply to the phronimids, oxycephalids, phrosinids, and palinurids (the last is represented in the net catches only as translucent larvae).

The second and fourth points (the net catching at greater depth and slower speed than the tunas) could explain the greater occurrence of active epipelagic fish (scombrids, scomberesocids, thunnids, exocoetids, coryphaenids, polynemids, carangids, and perhaps others) in tuna-caught than in net-caught micronekton. The Exocoetidae (flying-fishes) are a good example: only one small speci-

men was taken in the 131 hauls of the 1.5-m. net, but several, including large ones, have been taken at various times in hauls of the high-speed net. Under the circumstances in which we have used these nets, the high-speed net is obviously the more efficient (behaving more like a tuna) for catching exocoetids, in spite of its smaller mouth. This greater efficiency arises from the greater speed of hauling or because we have towed it only in the upper 10 m., where exocoetids are probably most abundant.

The apparent scarcity of enoploteuthid and cranchiid cephalopods in tuna stomachs might not be real, because of their inclusion in unidentifiable material, as noted in the fifth point above. This explanation might also apply to leptocephali.

For some of these reasons, it is perhaps surprising that the percentages for some other groups (Galatheidae, Euphausiidae, Squillidae, and *Vinciguerrria*) agree as well as they do in the net-caught and tuna-caught micronekton; euphausiids certainly, and probably *Pleuroncodes planipes* (Longhurst, 1967), and *Vinciguerrria* (Ahlstrom, personal communication), are more abundant near the surface by night than by day. These kinds of micronekton sometimes occur at the sea surface in full daylight, however, and possibly their daytime submergence is not so great or so regular as to make them entirely unavailable to tunas.

It is possible that records of the percentages of individual species of Crustacea, which are mostly not available at present, would remove some of the similarities which appear to exist between net catches and contents of tuna stomachs—for example, in the euphausiids. Such records would not affect the galatheids greatly, however, since nearly all were *Pleuroncodes planipes* in both the net catches and the contents of tuna stomachs. *Vinciguerrria* would not be seriously affected either, because all of Alverson's specimens and most of mine were *V. lucetia*, although my material included a few *V. nimbraria*, and several specimens that were doubtful (see Ahlstrom and Counts, 1958, concerning *Vinciguerrria* in the eastern Pacific).

These considerations give insufficient reason to doubt the commonly held opinion that yellowfin and skipjack tuna feed on most kinds of micronekton which occur in their habitat, with the qualification that the prey must occur under conditions in

which the tuna could perceive them visually. The tunas are opportunistic feeders, within their sensory limitations. The only important exception to this generalization is the apparent failure of yellowfin tuna to eat euphausiids, which are much used by skipjack tuna. Efficient capture of euphausiids by large pelagic fish may require special behavior, however (see Blackburn, 1957, on the gempylid scombriform *Thyrsites atun*), and it is possible that these behavior patterns have not evolved in yellowfin tuna.

COMPARATIVE ABUNDANCE OF POTENTIAL TUNA PREY BY AREAS

From tables 8 to 14, and the tables of Alverson (1963a) which show percentage composition of tuna stomach contents for other areas, a list was made of families and other groups which made up 5 percent or more by volume of stomach contents of yellowfin and skipjack tunas in any one of the areas 1 to 14.⁶ These groups were considered potential tuna prey in all areas where they occur. Groups which were not represented in the net hauls—the Engraulidae and Polynemidae—were disregarded. This omission left the following groups, which represent kinds of potential tuna prey which the net is capable of catching to some extent in standard night hauls:

<i>Yellowfin tuna prey</i>	<i>Skipjack tuna prey</i>
Fish:	Fish:
Gonostomatidae	Gonostomatidae
Myctophidae	Myctophidae
Exocoetidae	Exocoetidae
Thunnidae	Thunnidae
Carangidae	Serranidae
Stromateidae	Scomberesocidae
Coryphaenidae	Trichiuridae
Ostracidae	
Tetraodontidae	
Crustaceans:	Crustaceans:
Galatheidae	Galatheidae
Portunidae	Portunidae
Sergestidae	Euphausiidae
Squillidae (adults)	Squillidae (larvae)
	Phrosinidae
Cephalopods:	Unidentified crab
Ommastrephidae	megalo

The total volume of net-caught potential prey for yellowfin tuna and for skipjack tuna was standardized (as explained above) for each area (1 to

⁶ Stromateidae (table 3, and below) are equivalent to Nomeidae as listed by Alverson.

18). Although it cannot be assumed that each of the prey groups was captured by the net or by the tunas with the same degree of efficiency in each area, the standardized volumes may be compared from area to area (for the prey of each tuna species separately), to indicate broad quantitative differences and similarities among areas in the extent to which they support standing crops of potential tuna prey. Obviously, these volumes do not represent absolute concentrations of tuna prey.

Standardized volumes of skipjack tuna prey were higher than those of yellowfin tuna prey (table 15) for most areas, because they included euphausiids and squillid larvae. Volumes in area 1 were by far the highest, because of the great abundance of *Pleuroncodes planipes*; they are further discussed below. The next highest volumes were in areas 8 and 10, but they are based on only two hauls per area and may, therefore, not be representative; volumes for areas 9, 14, and 15 are likewise ignored because only three or four hauls were made per area.

TABLE 15.—Standardized volumes (ml./10³m.³) of total potential prey of yellowfin and skipjack tuna as taken in standard night hauls of the 1.5-m. net, for the areas shown in figure 5

[Actual volumes (ml.) from table 3, other data from table 1; for further explanation see text]

Area	Hauls	Total time	Prey of yellowfin tuna		Prey of skipjack tuna	
			Actual	Standardized	Actual	Standardized
	Number	Minutes	Ml.	Ml./10 ³ m. ³	Ml.	Ml./10 ³ m. ³
1.....	21	984	16,951	63.7	18,497	69.5
2.....	6	383	674	6.5	716	6.9
3.....	18	839	845	3.7	1,255	5.5
4.....	29	1,546	3,277	7.8	3,039	7.3
5.....	10	565	747	4.9	748	4.9
6.....	5	262	527	7.5	961	13.5
8.....	2	96	318	12.2	428	16.5
9.....	3	195	28	.5	35	.7
10.....	2	132	481	13.4	501	13.9
11 and 12.....	6	387	455	4.3	528	5.0
14.....	4	200	152	2.8	318	5.8
15.....	3	194	270	5.1	274	5.2
16.....	7	435	418	3.5	437	3.7
17.....	7	333	414	4.6	414	4.6
18.....	8	406	170	1.6	410	3.7
Total.....	131	-----	-----	-----	-----	-----

Comparisons may now be made between volumes for areas 1, 2, 3, 4, 5, 6, and 11-12, which have a significant commercial surface fishing for yellowfin and skipjack tunas and volumes for areas 16, 17, and 18, in which there is no significant fishery (see Alverson, 1960, 1963b, for distribution of the surface fishery). The lowest volume of yellowfin tuna prey in an area which supports a fishery was

3.7 ml. per 1,000 m.³, in area 3; the lowest for skipjack tuna prey was 4.9 ml. per 1,000 m.³, in area 5. Volumes for area 16 were slightly below, and those for area 18 well below, these figures; but in area 17 the volume was higher than 3.7 for prey of yellowfin tuna and only slightly lower than 4.9 for prey of skipjack tuna.

Such small differences among areas should be interpreted very cautiously, for reasons given above. It could be argued, however, that area 17 has a sufficiently high standing crop of tuna prey to support a standing crop of yellowfin tuna, and possibly one of skipjack tuna, which might profitably be fished. Of course, the presence of an adequate crop of tuna food does not guarantee the presence of tuna, as is shown by the general scarcity of skipjack tuna in areas 3 and 4 in the years in which the micronekton was collected (Alverson, 1960, 1963b); high sea temperatures may have been limiting in those years, however (Blackburn and associates, 1962; Blackburn, 1963). A more conservative conclusion from the data of table 15 is that some areas west of the existing surface fishery might support commercial surface-fishing operations and should be further explored; and that area 17 is likely to be the best and area 18 the poorest of the three areas considered, as far as abundance of yellowfin and skipjack tunas are concerned.

A Japanese commercial subsurface hook fishery for yellowfin tuna exists at about the same latitudes as area 17; it is located west of area 17 but seems to be extending into that area. Similar fishing is carried on west of, and to some extent in, area 16, but the catch per unit of fishing is lower than in area 17. No longline fishery exists in or near area 18 (Suda and Schaefer, 1965). Skipjack tuna are not commonly taken by subsurface hooking.

The high standardized volumes of potential tuna prey in area 1 warrant comment. Although area 1 is eutrophic, its mean rate of primary production appears to be comparable with that of some other areas, such as 5 and 6, in which tuna prey are much scarcer (Holmes, 1958; Hela and Laevastu, 1962; Blackburn, 1966b). The special feature of area 1, as far as trophic relationships of yellowfin and skipjack tunas are concerned, appears to be the presence of an abundant herbivore, *Pleuroncodes planipes*, which is large enough to release

feeding behavior in tunas. By feeding on this animal, yellowfin and skipjack tunas probably consume a much greater fraction of the organic material produced by photosynthesis in this area than they do in other areas where herbivores are small and carnivores make up most of the tuna diet (see King and Iversen, 1962, table 15, for probable trophic levels of several groups of tuna prey listed above).

QUANTITATIVE COMPARISON OF CATCHES BY 1.5-M. AND HIGH-SPEED NETS

Reference was made previously to qualitative differences between the catches of the 1.5-m. net and the high-speed net; the example given was the greater representation of flyingfish in catches of the high-speed net. The high-speed net was hauled much faster and much closer to the sea surface, on the average, than the 1.5-m. net. It is of interest to compare quantitatively certain areal distributions of micronekton as measured by the two nets for the cruises (TO-59-2 and TO-60-2) for which both sets of material have been fully worked up. The volumes were standardized, as explained earlier, so that all volumes for both nets are comparable in ml. of micronekton per 1,000 m.³ of water strained.

Figure 17 summarizes the distribution of total micronekton (fish, crustaceans, and cephalopods combined) in standard night hauls of the 1.5-m. net on cruise TO-60-2; the volumes are the sum of the volumes shown for the same stations in figures 6, 7, and 8. Figure 18 gives similar information for night hauls of the high-speed net (only hauls lasting between 2½ and 3½ hours) on the same cruise.

As far as they are comparable, figures 17 and 18 show similar trends in distribution of micronekton from place to place within the area, especially from onshore (high volumes) to offshore (low volumes) for the area as a whole. Standardized volumes for the 1.5-m. net, however, tend to be about 9 or 10 times higher than those of the high-speed net, in the same area on the same night.

Figure 19 shows a similar comparison, for part of cruise TO-59-2 for catches of red crab (*Pleuroncodes planipes*) only. As far as the 1.5-m. net and high-speed net catches occur in the same

areas, they are broadly comparable in general distribution—particularly as between the area east of long. 112° W., where the crabs were scarce, and the rest of the region, where they were abundant. It is again evident that the volumes from the 1.5-m. net were generally much higher than volumes from the high-speed net when both were available at the same time and place.

The reason for the difference between the volumes is uncertain. Possible reasons that have been advanced are: (1) the catches in the high-speed net tend to get shredded by the fast towing so that much material is lost through the meshes; (2) micronekton is actually scarcer at 10 m., where the high-speed net fishes, than it is over the whole water column 0-90 m., where the 1.5-m. net fishes; and (3) the micronekton at 10 m. is disturbed by the ship, and some of it submerges or escapes laterally before the net reaches it. Inspection of catches shows that the first point probably does not apply to the extent that would be required to explain the observed difference, although it does apply to some extent; for instance, it is common to find fish reduced to skeletons in the high-speed net. There is no information on which to base a judgment on the other points. Aron (1962b) noted that catches of the Isaacs-Kidd midwater trawl were invariably low when the net was towed at the surface and attributed this effect to disturbance by the ship.

SUMMARY

Micronekton (fishes, crustaceans, and cephalopods about 1 to 10 cm. long) was collected on oceanographic cruises in most parts of the eastern tropical Pacific Ocean, mainly from 1958 to 1961. The most commonly used collecting method was to haul a large net (mouth 1.5 m. square; length about 5.8 m.) of uniform mesh size obliquely through the upper 90 m. of water at night, at a ship speed of 5 knots. Catches (total micronekton and its family components) were measured by displacement volume; these volumes were then standardized to 1,000 m.³ of water strained, by using data on the length of the haul and an empirical filtration coefficient of 76 percent. These measurements of standing crop of micronekton are superior to those that can be obtained with mixed-mesh nets or trawls of the same general size.

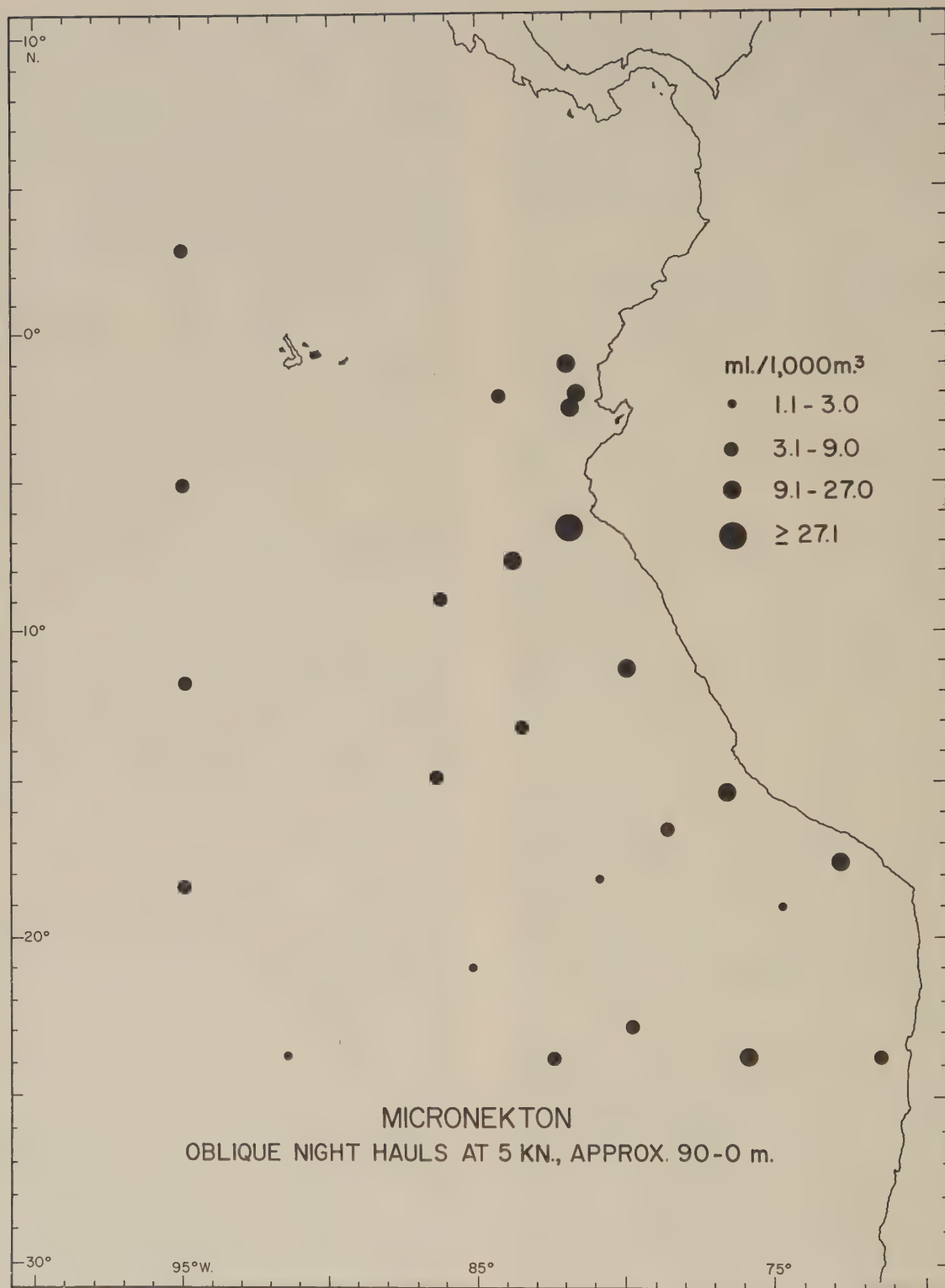


FIGURE 17.—Distribution of standing crop (standardized volume) of total micronekton taken in standard night hauls of the 1.5-m. net on cruise TO-60-2.

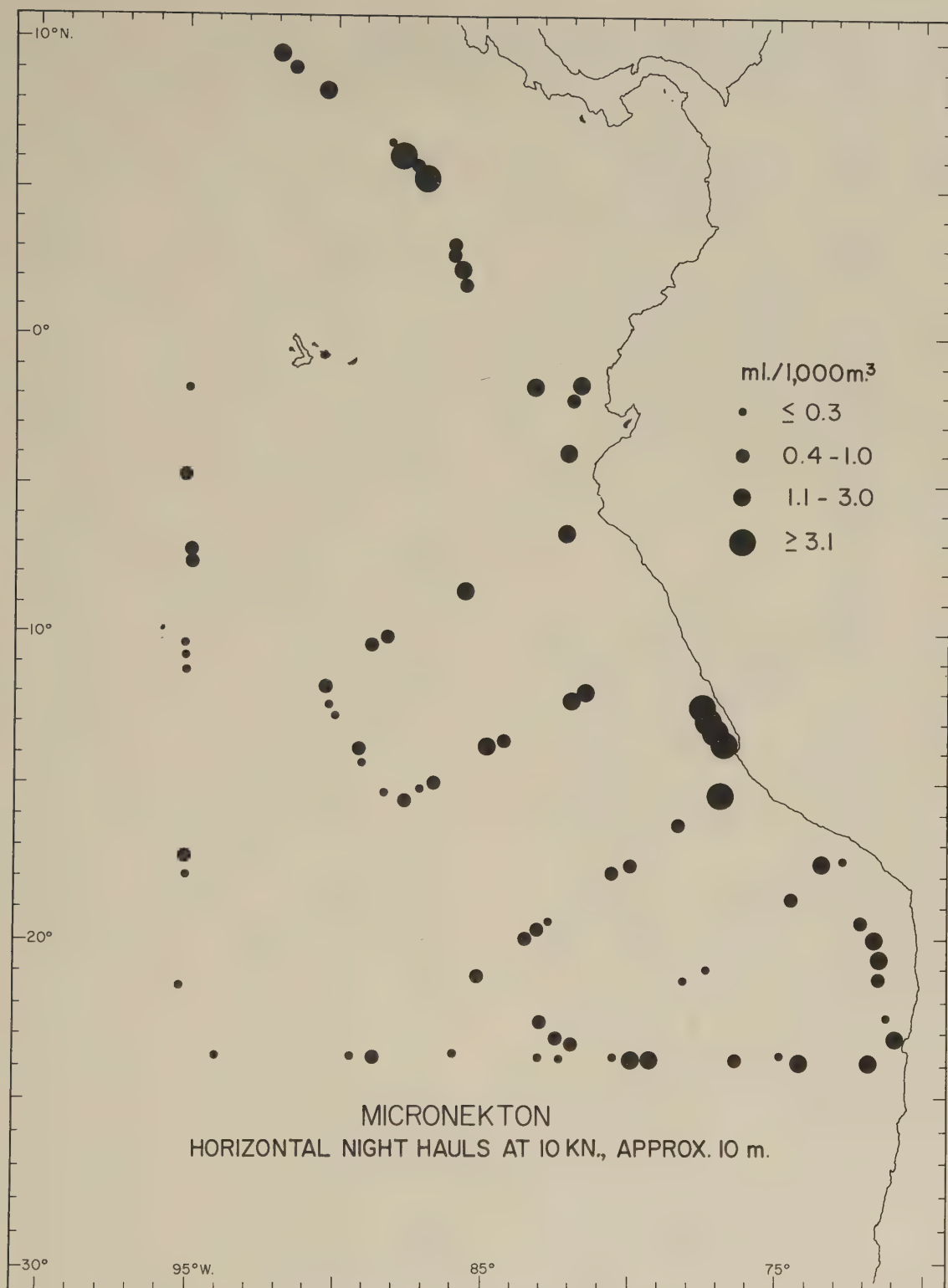


FIGURE 18.—Distribution of standing crop (standardized volume) of total micronekton in night hauls of 2½ to 3½ hours' duration with the high-speed net on cruise TO-60-2.

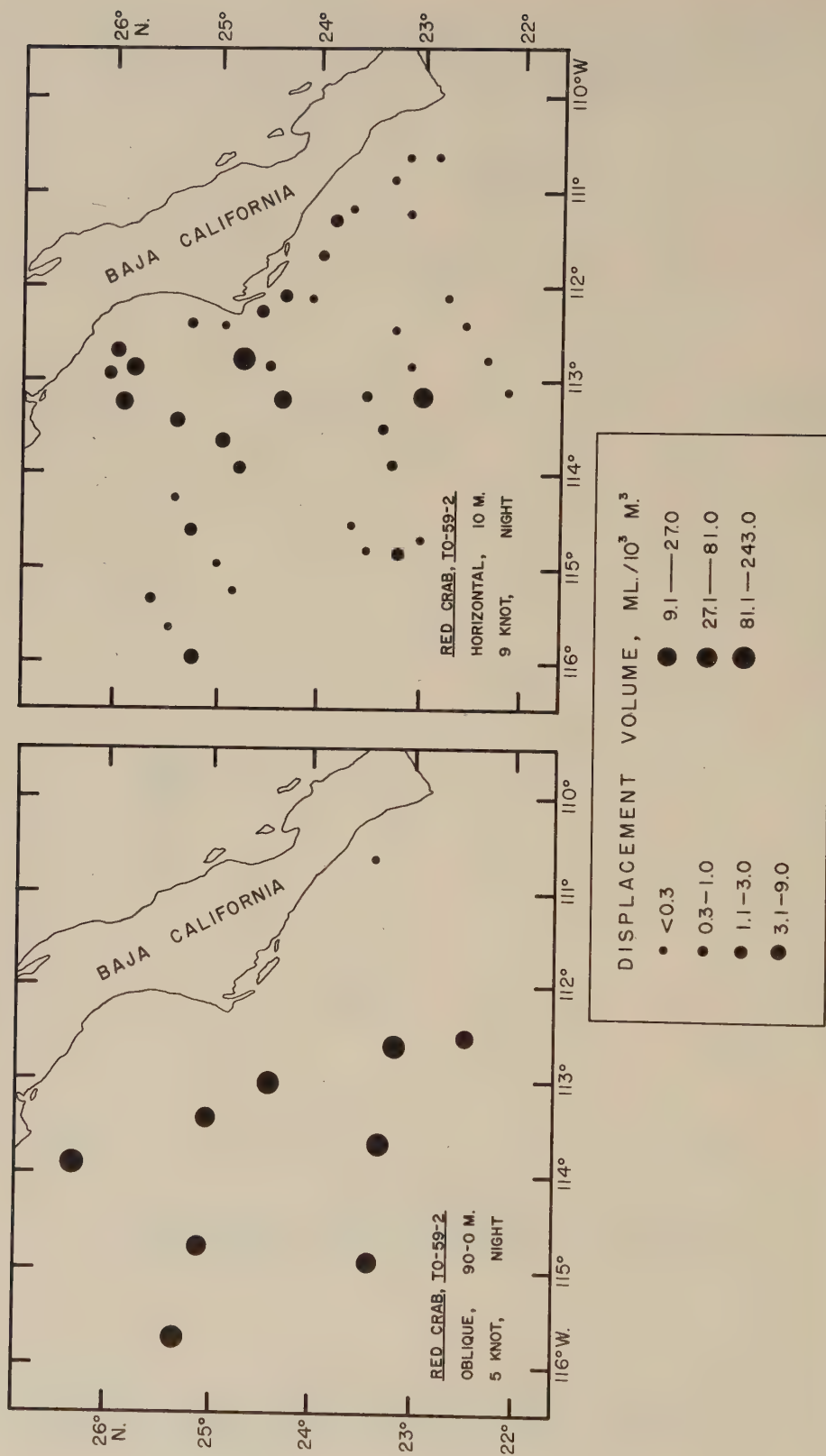


FIGURE 19.—Distribution of standing crop (standardized volume) of *Pleuroncodes planipes* taken in standard night hauls of the 1.5-m. net (left) and in night hauls of the high-speed net (right), on part of cruise IO-59-2. Duration of hauls of the high-speed net ranged from 2 to 3 hours.

Ten families (Myctophidae, Gonostomatidae, Galatheidae, Euphausiidae, Penaeidae, Squillidae, Portunidae, Sergestidae, Enoploteuthidae, and Cranchiidae), and one suborder (Apodes; leptocephali only), which was not sorted to family, made up 93.4 percent of the total volume of micronekton collected in 131 standard night hauls. The areal distribution of standing crop was broadly the same for most of the groups; crops were higher onshore than offshore and highest in onshore areas where physical processes that enrich the upper water layer are known to operate. Three groups of crustaceans (Galatheidae, Portunidae, and adult Squillidae) were confined to relatively small, mainly onshore, areas. The data were insufficient for comparison of standing crops at different seasons, except in the Gulf of Tehuantepec, where the crops appear to fall a few months after enriching physical processes decline.

The composition of the net-caught micronekton was compared with the composition of stomach contents of yellowfin and skipjack tunas as published elsewhere, for certain areas of the eastern tropical Pacific. As compared with tuna, the nets caught different fishes, but broadly similar crustaceans. The differences are attributed to: the fact that the nets catch large quantities of night-rising mesopelagic fishes which do not occur in the tunas' habitat by day, and are probably not seen by the tunas at night; leptocephali are probably not perceptible to tunas in the daylight, since they are translucent; and the more active epipelagic fishes are more efficiently caught by tunas than by nets.

Families which made up at least 5 percent of the stomach contents of yellowfin or of skipjack tuna in any area were considered to be potential prey for the species. To the extent that the net sampled these families, comparisons could be made of potential tuna prey in ml. per 1,000 m.³ in different areas (with and without a commercial fishery), for which net data were available. The comparisons suggested that one virtually unfished area supports a crop of potential prey of yellowfin tuna which is higher than that in one of the well-fished yellowfin tuna areas; and also a crop of potential skipjack tuna prey which is nearly as high as that in one of the well-fished skipjack tuna areas. This area, which lies west of the existing fishery area for surface tuna along the coasts of Ecuador and northern Peru, might, therefore, con-

tain yellowfin or skipjack tuna in commercial quantities. Crops of potential tuna prey are much higher off western Baja California than elsewhere; the principal prey species there is the galatheid pelagic crab *Pleuroncodes planipes*, which is in part a herbivore (giving the tunas a more efficient food chain than in most other areas) and extremely abundant.

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SUPERSATURATION OF ATMOSPHERIC GASES IN THE COASTAL WATERS OF THE GULF OF MAINE

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ABSTRACT

Year round observations of dissolved oxygen in 1964-67 regularly revealed supersaturation of 120 to 150 percent during the spring and summer. Seasonal variations took the form of a sinusoidal cycle that showed definite phase relations to temperature. Comparisons with data for offshore dissolved oxygen showed that in general the coastal waters were more highly supersaturated.

Supersaturation of oxygen in marine waters, particularly in coastal areas, is not uncommon, and references to it are numerous in the literature. Its effect on marine life has apparently not been investigated, nor are there adequate records for comparison with observed fluctuations in distribution or abundance of organisms.

The coastal waters of the Gulf of Maine support several fisheries, chief among which are those for lobsters (*Homarus americanus* M. Edw.) and for Atlantic herring (*Clupea harengus harengus* L.). The herring fishery in particular suffers from irregular periods of poor catches due to unfavorable distribution (hence, lack of availability) as well as to low abundance. The causes for these irregularities in availability are not known.

To seek possible relations between herring distribution and hydrography, the Bureau of Commercial Fisheries Biological Laboratory in Boothbay Harbor, Maine, is investigating several aspects of the hydrography of coastal waters. Interest in dissolved oxygen stemmed primarily from an outbreak of gas disease in the laboratory aquaria in June 1964. At that time the sea water in these aquaria effervesced with tiny bubbles; several herring died from gas disease and many more showed the typical symptoms—disorientation, exophthalmia (popeye), and bubbles in the fins and lateral line organs. This disease is frequently a result of supersaturation caused by defects in the

Nitrogen measurements made in conjunction with those of oxygen led to the conclusion that oxygen supersaturation was usually due to photosynthesis, but occasionally supersaturation of both gases indicated some physical cause.

water pumping system. Careful inspection of our system, however, revealed no defects. Furthermore, Winkler tests of water taken directly from the harbor as well as that supplied through the pumping system showed substantial supersaturation of oxygen. Whether the supersaturation was due to excessive dissolved air, or to oxygen only, was not determined at the time as no equipment was then available at the laboratory for measuring nitrogen. Routine measurements of dissolved oxygen began in the early summer of 1964, but nitrogen measurements were not undertaken until 1965.

Although some data on dissolved oxygen have been published for the Gulf of Maine (Gran and Braarud, 1935; Rakestraw, 1933; Colton, Marak, Nickerson, and Stoddard, 1968), these records are limited to short periods during a few years and cover mainly the open waters of the Gulf rather than the inshore regions. Only occasional measurements have heretofore been made in the coastal waters.

METHODS

Water samples for oxygen analysis were not taken according to a regular schedule, but were spaced to provide a fair coverage of each month. Samples were taken three to five times per week in spring and summer and about once a week in fall and winter. The most conveniently and frequently sampled source was the water pumped into the laboratory from a depth which varied accord-

ing to tide from about 3 to 6 m. The harbor water was sampled directly with a dissolved oxygen sampling bottle¹ at a depth of 2 m. at the same time the pumped water was sampled, except that during the first winter only one sample was taken each month.

For the first 6 months, samples were analyzed with a polarographic dissolved oxygen meter, but this method proved somewhat unreliable at low temperatures. After the first winter, all determinations were made by the unmodified Winkler procedure. Because the Winkler method has several sources of error, the routine technique was periodically checked on standards of water saturated with air under controlled conditions. The errors averaged about ± 0.1 p.p.m.; I did not consider them serious for the purpose of this study. Solubility data for oxygen were obtained from the tables of Green (1965).

Measurements of dissolved nitrogen were not made during the first year (1964). In 1965 a few determinations were made with a manometric Van Slyke apparatus, and in 1966 and 1967 periodic nitrogen determinations were made according to the micro-gasometric method of Scholander, Van Dam, Claff, and Kanwisher (1955). Solubility data for nitrogen were obtained from the tables of Rakestraw and Emmel (1938).

The amount of dissolved oxygen sometimes varied considerably during the day. This fluctuation reflects in part the diurnal cycle of oxygen sometimes called the "oxygen pulse." To obtain comparable measurements from day to day, samples were taken in the afternoon, when concentrations of dissolved oxygen were approaching their maximum. Tides also caused some variation that was reflected as irregularities in the seasonal trends.

OBSERVATIONS IN 1964

The highest oxygen concentration in the laboratory water during 1964 was 12.7 p.p.m. on June 23; the saturation was 153 percent. At the same time, the oxygen in the surface water at Boothbay Harbor was 10.8 p.p.m. and the saturation was 131 percent. Daily maxima of 130 to 140 percent saturation were frequent during June, but thereafter during the summer the levels decreased and fluctuated between 110 and 120 percent saturation.

Samples taken elsewhere along the coast in July ranged from 107 to 115 percent saturation in Casco Bay, 100 to 104 percent saturation in Penobscot Bay, and 102 to 112 percent saturation along the eastern Maine coast. Unfortunately, these measurements were not made until after the extremely high values of dissolved oxygen at Boothbay Harbor had diminished; hence, they may be lower than would have been observed earlier in the year.

OBSERVATIONS IN 1965

Oxygen measurements were discontinued toward the end of 1964, but were resumed in January 1965. The water remained close to 100 percent saturation during the winter, but in mid-March the first of a series of peaks in both concentration and saturation appeared; concentration reached 13.5 p.p.m. and saturation 120 percent. The second major peak was in early May when the concentration was 13.5 p.p.m. and saturation over 130 percent. At that time dissolved nitrogen was also high (in excess of 120 percent saturation) for a few days. Thereafter, the concentration of dissolved oxygen decreased slowly and irregularly until the end of July, but because of rising temperature the saturation remained between 120 and 130 percent. Except for a few days in May, dissolved nitrogen, whenever measured, was close to 100 percent saturation.

Winds can sometimes produce dramatic changes in the amounts of dissolved oxygen. A precipitous decrease in dissolved oxygen took place after a strong northwest wind on August 28 and 29; the concentration dropped to 7.3 p.p.m. and saturation to less than 90 percent, but rose shortly to levels as high as before. A second northwest wind-storm on September 26 again dropped the oxygen to below 100 percent saturation where, except for a slight rise during October, it remained for the rest of the year.

For localities other than Boothbay Harbor, saturations in June were 114 to 119 percent in Casco Bay and 117 to 127 percent along the eastern Maine coast.

OBSERVATIONS IN 1966

Saturation of oxygen began to rise above 100 percent late in January. Three major peaks occurred during the spring. In the laboratory water supply these reached 128 percent in late March, 128 percent again in mid-April and 137 percent in

¹Type recommended by A.P.H.A. Standard Methods of Water Analysis.

mid-May. The May peak was the highest for the year (13.6 p.p.m., 137 percent saturation) in the laboratory supply water, but the harbor surface did not reach its annual maximum until June 8 (12.3 p.p.m., 133 percent saturation). Thereafter the dissolved oxygen in both water sources decreased irregularly throughout the summer, although the highest average for August was in 1966. Throughout the fall and winter, saturation was usually between 90 and 100 percent.

OBSERVATIONS IN 1967

The dissolved oxygen remained near or below saturation through February, but the concentration reached a record high for the period of study: 14.8 p.p.m. on March 27. Despite the relatively low temperature, saturation reached 130 percent at this time. The next major peak appeared during the third week in May, when the concentration reached 13.5 p.p.m. and saturation 135 percent. Values for pumped water and harbor surface water differed only slightly. As in the 2 preceding years, dissolved nitrogen rose to about 120 percent saturation for a few days in May.

By the end of June the supersaturation of oxygen declined markedly, and the July average was the lowest for that month in the 4-year period. In general, oxygen supersaturation was lower during the whole summer of 1967 than in the 3 preceding years. This drop may have indicated a long-term downward trend, or could have been due to an unusual amount of cloudy or foggy weather.

ANNUAL TRENDS AND COMPARISON WITH OFFSHORE WATERS

The seasonal and annual trends in temperature and in oxygen concentration, percentage saturation of oxygen, and temperature are shown in figure 1. The values shown are averages of all afternoon measurements made each month. They can be considered to be the monthly means of daily maxima.

A study of the figure reveals several points of interest. Both concentration and saturation show a cyclic pattern that bears some relation to temperature. Oxygen concentration tends to be highest when the water temperature is low, but the peaks lag the temperature minima by about a month. Percentage saturation is highest during periods of rising temperatures. The probable reasons for these

phase relations are that oxygen is more soluble at low temperatures but the peak of oxygen production by photosynthesis occurs later than the time of minimum temperatures. Maximum concentrations, therefore, occur when the interaction of high solubility and maximum production is optimal. Maximum saturation is similarly the result of optimal interaction between high production and low solubility. Saturation is further increased when the rate of warming outpaces the rate at which the dissolved gas can come into equilibrium with the atmosphere.

The supersaturation of oxygen appeared to be somewhat higher at Boothbay Harbor than at other localities along the coast, although the number of samples taken elsewhere may not have been sufficient to provide a fair comparison. Values for coastal waters were generally higher in 1965 and 1966 than those observed for comparable periods in offshore waters during the *Albatross IV* cruises (Colton et al., 1968). In 1965 no offshore samples exceeded 120 percent saturation in May and June, and in 1966 only 3 percent of all samples from the top 20 m. in the open Gulf of Maine were greater than 120 percent. At Boothbay Harbor during the comparable period of both years, 78 percent of the samples in 1965 and 82 percent in 1966 exceeded 120 percent saturation. Elsewhere along the coast during a comparable period, 14 percent of the samples in 1965 and 43 percent of those in 1966 showed over 120 percent saturation.

CAUSATIVE FACTORS

Oxygen supersaturation in the sea can result from several processes, of which two have major significance. The most important is probably the actual increase in oxygen concentration resulting from photosynthesis; the other is a change in the physical properties of the water which affects the solubility of gases. Air that diffuses into water from the atmosphere at the sea surface can produce 100 percent saturation of oxygen and nitrogen at the ambient temperature, salinity and barometric pressure; if these physical properties change rapidly, the water can become at least temporarily supersaturated. Rapid warming of saturated water, or the mixing of warm and cold saturated water results in supersaturation until the gases are able to once again achieve equilibrium with the atmosphere.

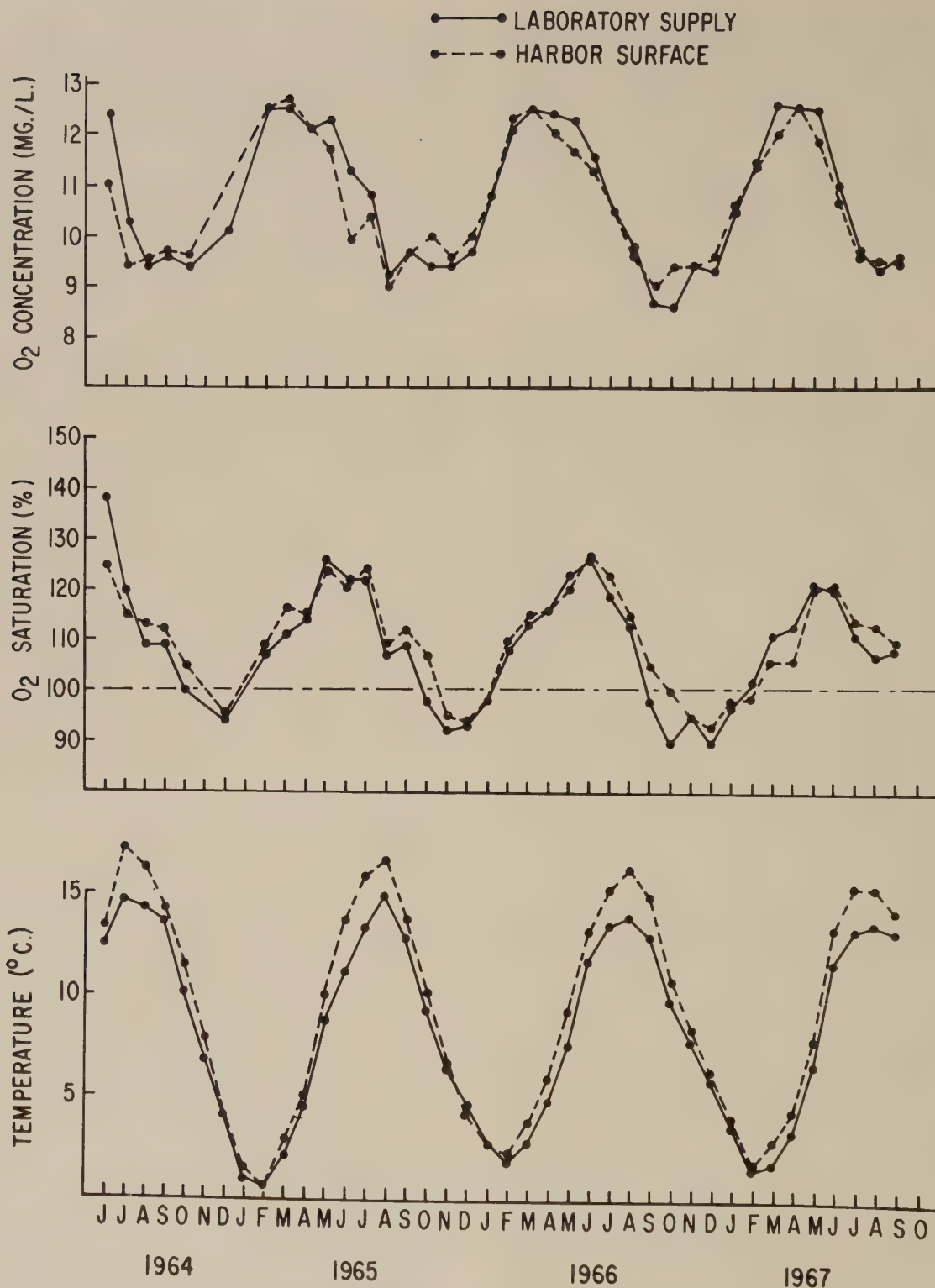


FIGURE 1.—Monthly means of daily maximum concentration and percentage saturation of dissolved oxygen and corresponding mean water temperatures at Boothbay Harbor, Maine, 1964–67.

TABLE 1.—Percentage saturation of nitrogen and concentrations of oxygen in excess of saturation according to source, calculated from observed nitrogen and oxygen concentrations. P: photosynthetic oxygen, A: atmospheric oxygen. Entries for each month are given chronologically but the dates for each entry do not correspond exactly from year to year; approximate time of month is indicated by the position of each entry in a column.

Year	1965			1966			1967		
	N ₂ saturation	Excess O ₂		N ₂ saturation	Excess O ₂		N ₂ saturation	Excess O ₂	
		P	A		P	A		P	A
Month	Percent	Ml./l.		Percent	Ml./l.		Percent	Ml./l.	
March	98	None	None	102	0.15	0.15	109	0.10	0.75
April	104	0.80	0.30	98	.75	None			
	113	None	.65						
	109	.55	.70						
	105	.25	.30						
May	106	1.20	.30	100	1.75	None	104	None	.27
	127	None	1.80	108	None	.45	113	None	.70
	127	.60	1.90	113	None	.60	110	.55	.80
				106	1.50	.45			
				109	1.75	.50			
				116	1.60	1.15			
				116	.95	1.20	117	1.05	1.25
				112	1.30	.80			
				114	1.20	.95	121	None	1.45
	103	2.05	.15	110	.90	.70			
				109	.70	.70	106	1.05	.50
June	85	1.25	None	107	.40	.50			
	104	.35	.25	107	1.30	.50			
	96	1.35	None	100	1.10	.10			
	97	1.45	None	104	.40	.35	107	None	.55
	101	1.40	.10	101	.90	.10	105	.25	.50
	98	1.35	None	102	.50	.20			
	94	1.00	None	101	.30	.10			
July	92	1.15	None	109	.35	.65			
				108	.35	.60			
				109	None	.75			
				108	.05	.60	106	None	None
				111	.05	.75	108	None	.25
				110	None	.55			
				112	None	.50			
				115	.20	.95	111	None	None
August	109	.60	.60	110	None	.40	111	None	.30
				117	None	.60	107	None	None
	98	.55	None	111	None	None	111	None	None
				113	None	None	106	None	.30
				108	None	.35			
September	104	1.25	.30	112	None	None			
				108	None	.40			

Supersaturation arising from these two processes can be distinguished if the concentration of nitrogen is known. Nitrogen and oxygen which enter solution from the atmosphere bear a nearly constant ratio to one another, expressed by the equation $O_2 = .577 N_2 - .22$ (Rakestraw and Emmel, 1938). This equation indicates the amount of oxygen which ought to be in solution for any given concentration of nitrogen. Oxygen in excess of this amount represents that added by photosynthesis; the difference between the calculated oxygen concentration and the oxygen concentration at saturation represents the excess or deficit of atmospheric oxygen.

Nitrogen observations were made only intermittently in the present study; the observations, however, together with source composition of excess oxygen are given in table 1. As can be seen, the greatest nonphotosynthetic oxygen supersaturation and supersaturation of nitrogen occurred usually in April or May or occasionally in midsummer.

The physical causes of supersaturation could be intensified by the coastal topography. Numerous protected and shallow embayments permit rapid warming of the water; tidal movement is strong and conducive to the mixing of warm and cold saturated water, producing supersaturation of the mixture; warming of subsurface waters is a possible result of the flooding of sunheated tidal flats. I have no evidence that these particular processes are, in fact, the cause of nonphotosynthetic oxygen supersaturation, but they are theoretically possible.

ECOLOGICAL SIGNIFICANCE

The immediate question posed when the first indications of supersaturation were noticed was whether this situation was unusual or a regular annual occurrence. On the basis of 4 years of observations, the answer seems to be that it is a regular occurrence, although annual variations in the seasonal cycle are marked. Longer term trends may also be indicated in the basic annual cycles.

The duration and degree of supersaturation declined with each passing year of the period studied.

Strong annual variations in the degree of supersaturation could very probably produce fluctuations in the abundance and distribution of marine organisms if these organisms can be affected by supersaturation. The most marked effect of supersaturation on fish and other organisms is gas bubble disease. This disease, however, does not appear unless certain conditions obtain. By convention, the percentage saturation of dissolved gases in the sea is the ratio between the observed concentration at some depth and the concentration which would exist at the sea surface in equilibrium with the atmosphere at the same temperature and salinity as the depth in question. Thus, water at moderate depths may be supersaturated according to this definition and yet because of the hydrostatic pressure actually be capable of holding much more gas in solution. Ricker (1934) has called the degree of saturation which is related not to a theoretical surface value, but to the absolute capacity of water at a given hydrostatic pressure, the "absolute saturation." "Gas disease" due to supersaturation alone can occur only in absolute supersaturation. Furthermore, this supersaturation must be extremely high if gas disease is to be caused by oxygen. Observations have been made of gas disease occurring in the natural environment at oxygen saturations of 250 percent (Renfro, 1963) and over 300 percent (Woodbury, 1942). I have experimentally induced gas disease in herring (*Clupea harengus harengus*) at saturations of pure oxygen of 300 percent, but could not produce the symptoms at less than 200 percent saturation. Nitrogen, however, seems to be dangerous to fish at saturations of 125 percent or more (Marsh and Gorham, 1905; Egusa, 1959). In air-supersaturated water, I have experimentally induced gas disease at saturations of 120 percent nitrogen and 130 percent oxygen. In my experiments, the herring showed a definite tendency to avoid the supersaturated water, but only when the saturation levels were high enough to produce gas disease.

Gas disease can occur, furthermore, only when the total gas pressure in the water exceeds the combined hydrostatic and atmospheric pressures. When the concentration of any gas is increased by the displacement of another gas, gas disease is unlikely as long as the total gas pressure is not in-

creased. Fish have been exposed with little harm to oxygen saturations of up to 400 percent by bubbling this gas into the water at atmospheric pressure (Haempel, 1928; Bishai, 1960). Pathological symptoms occurred in some of Haempel's fish, but they seemed to be unrelated to gas disease.

The above evidence suggests very strongly that the levels of gas supersaturation along the Maine coast are not high enough to have a direct detrimental effect on fish in their natural environment. The situation under artificial conditions is much different, however. In aquaria, lobster pounds, and other similar installations where water is pumped from below the surface of the sea into relatively shallow tanks at sea level atmospheric pressure, any nominal supersaturation becomes absolute. This supersaturation, perhaps aggravated by elevations in temperature or by the pumping system, itself could produce lethal conditions as it did in our laboratory in the summer of 1964. The most likely effect of supersaturation on fish populations, if there is any effect at all, would probably be indirect, but lack of evidence to demonstrate such effects precludes useful discussion of them at this time. The facts do show, however, that a condition does exist, and recurs annually in more or less cyclic fashion, which could conceivably play a definite role in the ecology of marine organisms.

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RELATION BETWEEN TAIL LENGTH AND TOTAL LENGTH FOR THREE COMMERCIALLY IMPORTANT SPECIES OF PENAEID SHRIMP¹

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Length measurements of shrimp from commercial landings are an important source of biological information. Total length (tip of telson to tip of rostrum) is the measurement most commonly used, but it cannot be determined directly when fishermen separate shrimp "heads" (cephalothorax) and "tails" (abdomen) before they reach the docks. We determined the relations between tail length (anterior margin of first abdominal segment to tip of telson) and total length so that measurements obtained from headless shrimp could be converted to total lengths.

The relations were based on data from 1,581 brown shrimp, *Penaeus a. aztecus* Ives (86-225 mm., total length); 2,460 white shrimp, *P. setiferus* (Linnaeus) (74-213 mm.); and 1,909 pink shrimp, *P. d. duorarum* Burkenroad (82-194 mm.). The brown and white shrimp were caught off the Texas coast, and the pink shrimp were from the Tortugas grounds off Florida. Measurements were made to the nearest millimeter, and, when possible, equal

numbers of shrimp were measured in each 5-mm. total length group.

The relation between tail length and total length appeared to be linear for the range of sizes examined; a straight line was fitted to data for each sex of each species by the method of least squares (figs. 1 and 2). Formulas for the lines are presented in table 1.

TABLE 1.—Equations describing the relations between tail length and total length of pink, brown, and white shrimp

[Y = total length, X = tail length]

Species and sex	Equation	Standard error of regression coefficient	Number measured
Pink:			
Male	$Y = 8.762 + 1.547X$	0.008	802
	$X = -4.041 + .632Y$	.003	
Female	$Y = 4.506 + 1.628X$	.005	1,107
	$X = -1.923 + .607Y$	.002	
Brown:			
Male	$Y = 7.221 + 1.593X$	.009	598
	$X = -2.998 + .616Y$	.003	
Female	$Y = -1.085 + 1.710X$	.007	983
	$X = 2.029 + .576Y$	.002	
White:			
Male	$Y = 5.356 + 1.623X$	.004	1,214
	$X = -2.573 + .611Y$	.002	
Female	$Y = 2.882 + 1.672X$	.004	1,246
	$X = -1.154 + .594Y$	.001	

¹ Contribution No. 262, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas 77550.
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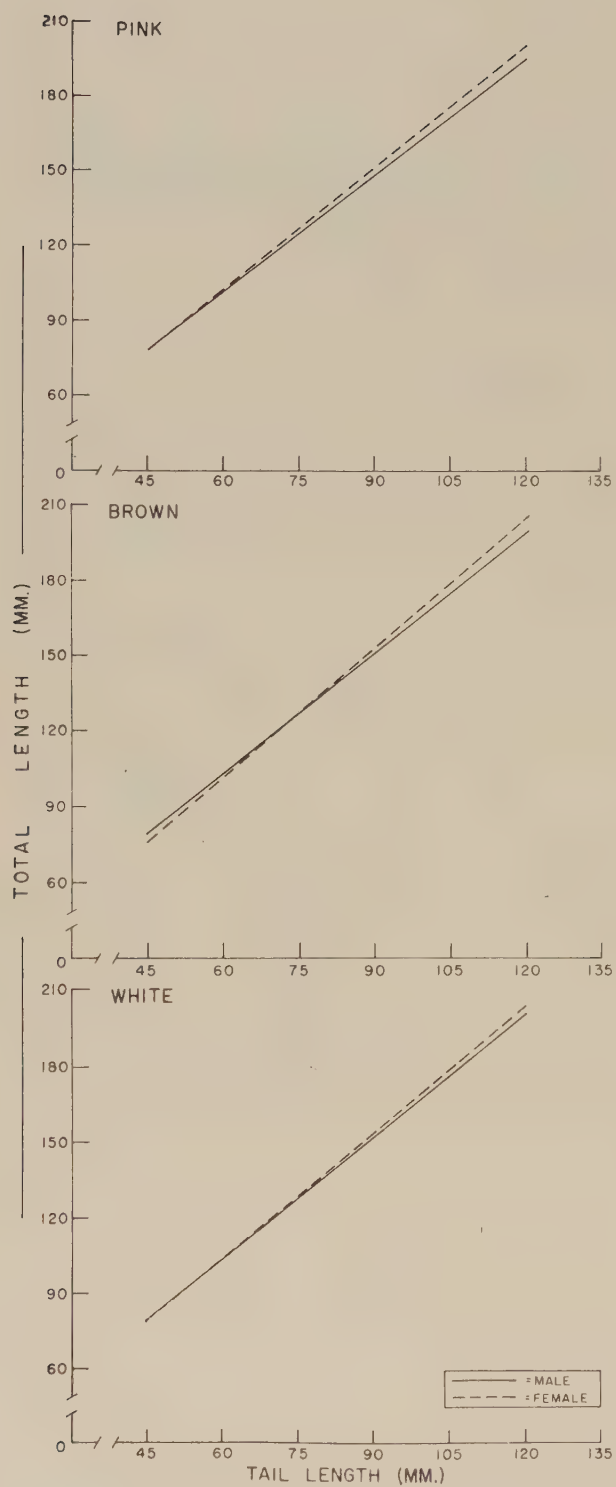


FIGURE 1.—The tail length-total length regression lines for pink, brown, and white shrimp.

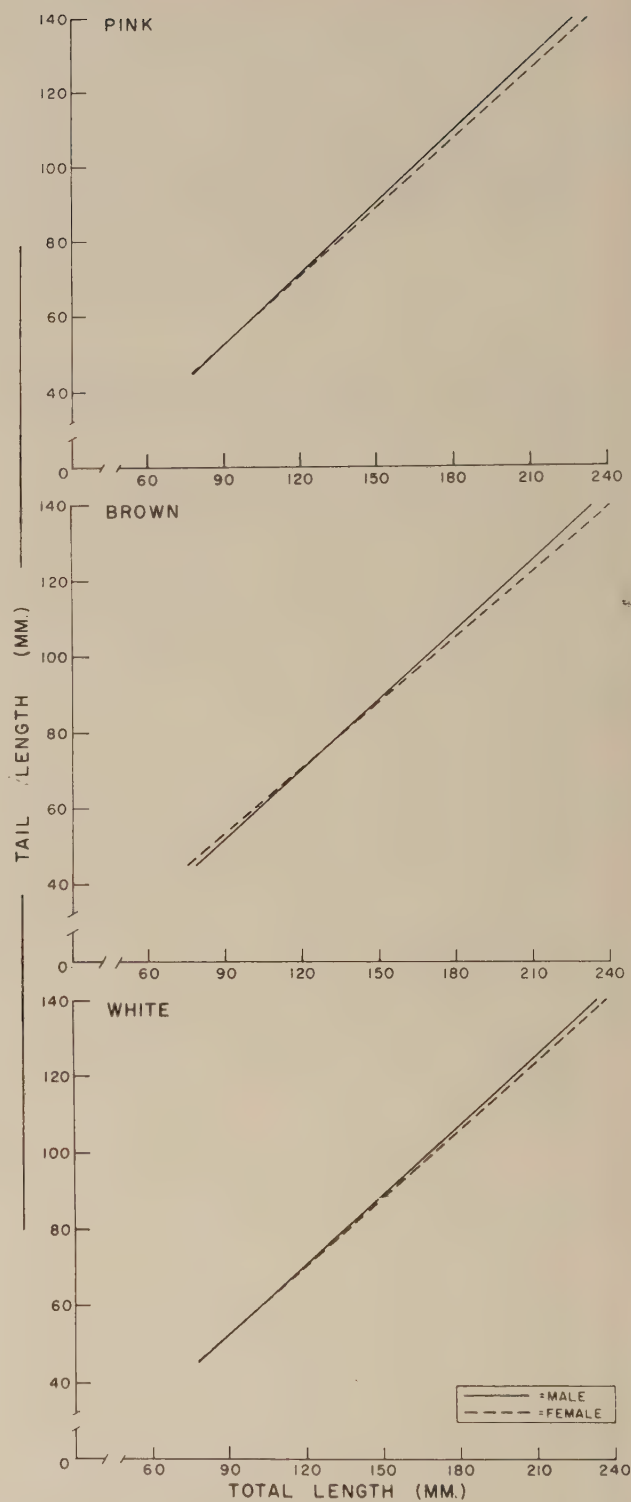


FIGURE 2.—The total length-tail length regression lines for pink, brown, and white shrimp.

SEA-STARS OF NORTH CAROLINA

BY I. E. GRAY,¹ MAUREEN E. DOWNEY,² AND M. J. CERAME-VIVAS³

ABSTRACT

Descriptions, keys to identification, and photographs are given for the 22 genera and 33 species of North Carolina asteroids. The starfish fauna is predominantly "southern." Eighteen species are distributed from North Carolina southward, nine range from North Carolina northward, and six occur both north and south of North Carolina. The affinities of the various

species to the principal marine biotic provinces are discussed. Thirteen tropical and subtropical species occur only in an extension of the Caribbean Province along the outer shelf. Only four of the 33 species on the Continental Shelf can be considered abundant: *Astropecten articulatus*, *Luidia clathrata*, *Astropecten americanus*, and *Asterias forbesii*.

Although isolated records exist, no previous attempt appears to have been made to bring together a list, with workable keys for their identification, of the asteroids that occur in North Carolina waters. Only the inshore, shallow-water species are well known. Pearse and Williams (1951) in their study of reefs off New River Inlet added two species new to North Carolina records and Cerame-Vivas and Gray (1966) listed six others. Sampling has been extensive in recent years; at least 33 asteroids are now known from the North Carolina Continental Shelf, and probably many additional species occur in deeper waters off the shelf. The need for identification sources for starfishes in this area has become acute because of the marked increase of interest in marine biology, the expansion of opportunity for oceanographic training, and the greater frequency of research cruises and offshore collecting by university classes in marine ecology and invertebrate zoology.

The present discussion is limited to the Asteroidea of the Continental Shelf; deep-sea species, even though in the latitude of North Carolina, are not included. The 200-m. contour, near the edge of the shelf, makes a convenient seaward boundary

of the area under consideration. Depth increases rapidly on the slope, and species of the continuously cold waters of the slope and beyond live in a different environment and more properly belong to the deep-sea benthos.

METHODS

SAMPLING PROCEDURES

Other than the fact that all starfishes are marine no single environmental condition is common to all species. Asteroids differ in habits, habitats, depths of water at which they occur, and in tolerance to adverse conditions. Consequently, no one sampling technique is adequate for all species. Hand-picking from jetties and the use of light dredges operated from small craft are satisfactory for collecting some species. Heavy gear is essential for dredging in deeper waters and on rocky ledges.

Especially useful to us, because they cut into the substrate, were the heavy Cerame-Vivas rock dredge (locally known as the C-V dredge) and the Cape Town dredge (also known as the Day dredge, because it was introduced by John Day of the University of Cape Town). The frame of the C-V dredge (Cerame-Vivas and Gray, 1966) was fashioned from scrap metal and, with lead shoes added, weighed over 200 kg. The leading edge consisted of a bulldozer blade estimated to cut into a substrate of hard-packed sand a minimum of 12

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cm. The mouth opening was slightly over 1 m. in width. This rugged dredge was used on rocky ledges as well as on level bottoms. Use of the smaller, lighter, and less rugged Cape Town dredge was limited mainly to level bottoms. Chartered shrimp trawlers and Duke Marine Laboratory's RV *Eastward* were used in the dredging.

For such forms as *Astropecten* and *Luidia* that glide over the sandy substrate and feed by ingestion of numerous small surface organisms, commercial trawls proved very satisfactory. Diving on reefs in relatively shallow water and using SCUBA (Self Contained Underwater Breathing Apparatus) produced some species not taken by other means, but this excellent collecting method was not used beyond a depth of 30 m.

Bottom photographs have sometimes helped demonstrate relative abundance, but only rarely can these be used alone for positive identification of species. Also, many sea-stars cannot be satisfactorily photographed because they bury themselves beneath the substrate and leave only an imprint to indicate their presence.

Probably some species which appear to be scarce would prove to be more abundant if more suitable methods for their collection were used, especially on reefs, ledges, and rock outcroppings too deep for normal SCUBA diving.

Not all parts of the shelf have been sampled with equal intensity, and our list of asteroids is probably incomplete. The most frequent collections have been made between the latitude of Oregon Inlet, well north of Cape Hatteras, and New River Inlet, well south of Cape Lookout. Material is more scanty from the area off Cape Fear and Frying Pan Shoals. Nevertheless, we believe that the data presented justify the assumption that most of the species to be found in North Carolina are included, since the areas that have been extensively sampled cover the principal marine biotic provinces. The most serious potential source of error lies not in the range of latitude sampled but in the lack of adequate collections from reefs and hard bottoms.

PRESERVATION TECHNIQUES

Starfishes should preferably be relaxed before preservation, but this is not always possible on shipboard. Some species normally remain flat, but in others the arms tend to curl. They can be relaxed and preserved in sea water in a flat enamel pan

large enough for the specimens to spread out without touching one another. The sea-stars flatten if magnesium sulphate (Epsom salt) is sprinkled on the water or if fresh water is added, a little at a time, until the sea water is replaced. Regardless of method, after relaxation is completed the water should be replaced by 70 percent alcohol or by 6 percent neutralized Formalin.⁴ Echinoderms should never be kept permanently in Formalin, however, as it destroys their calcite plates. Unfortunately, and perhaps unavoidably, alcohol removes much of the color. Usually it is more satisfactory to dry specimens after they have been preserved; this solves many storage problems. If later there is need to examine soft parts (e.g., to determine whether or not the podia have suckers), the whole specimen, or better still, a single arm can be soaked for a few hours in ordinary detergent. To examine underlying plates or other hard parts, soft tissue can be removed by dipping the appropriate part of the animal in household bleach. Bleach must be used carefully; excessive amounts can easily remove all connective tissue holding the plates together. The action of bleach can be quickly ended by rinsing the specimen in running water. It is best to treat only one arm of a specimen, as it may be desirable later to check certain anatomical features of the soft tissues.

To examine pedicellariae, one or two can be removed under magnification with fine forceps and placed on a glass slide with a drop of dilute bleach. Bleach will not always be necessary, as the valves of the pedicellariae are sometimes clearly visible without further treatment.

BIOGEOGRAPHICAL AREAS

Analysis of the distribution of any major group of benthic species on any segment of the North Atlantic Continental Shelf holds more than local interest. This is especially true of the North Carolina section of the shelf, which in any discussion of north-south distribution of species occupies a position of marked biogeographic importance. Located about midway on the U.S. Atlantic coast between temperate New England and subtropical Florida, the North Carolina shelf has several marine climates and associated temperature barriers within relatively few kilometers. Several capes,

⁴Trade names referred to in this publication do not imply endorsement of commercial products.

especially Cape Hatteras, project onto the shelf and divert water masses. The southwesterly flowing Virginian Coastal Current brings cool water from Cape Cod to Cape Hatteras before it is shunted seaward, and the warm Florida Current flows northeasterly and overlaps the outer edge of the shelf to a point well north of Cape Hatteras. The Carolinian Coastal Current, varying greatly in intensity depending on wind regimes, flows southwesterly from Cape Hatteras. The width of the shelf varies from less than 32 km. off Cape Hatteras to more than 80 km. across Onslow Bay. As shown by Cerame-Vivas and Gray (1966), boreal animals from the north and subtropical species from the south are both able to maintain themselves in North Carolina waters. This does not imply that the Continental Shelf of North Carolina is necessarily a transition zone between northern and southern species, but rather that species with different geographic affinities may occur in ecologically different areas in North Carolina waters, even at the same latitude.

Three marine biotic areas (fig. 1) have been recognized on the North Carolina Continental Shelf (Cerame-Vivas and Gray, 1966):

- A. The Virginian Province is a cold-water, wedge-shaped area that has its apex at Cape Hatteras and widens to the width of the shelf near the latitude of Oregon Inlet. This region is heavily influenced by the Virginian Coastal Current.
- B. The Carolinian Province extends southward from Cape Hatteras and occupies the inner two-thirds to three-fourths of the shelf. In addition to its own fauna, this area receives contributions from the Virginian Province in winter and from the Caribbean Province in summer.
- C. An extension of the Caribbean Province forms the outboundaries of both the Carolinian and Virginian Provinces and constitutes the outer shelf under the Florida Current. Northward it extends to the point where the Florida Current leaves the shelf. Because of the meanderings of the Florida Current over the edge of the shelf under different wind regimes (Bumpus, 1955; Bumpus and Pierce, 1955; Gray and Cerame-Vivas, 1963), neither the northern nor western limits of the Caribbean Province can be precisely defined.

The boundary between Virginian and Caribbean Provinces forms a much more formidable barrier to distribution than the barrier between Carolinian and Caribbean Provinces, which in summer is rather diffuse. The "Hatteras Barrier" between the Virginian and Carolinian Provinces is frequently broken in winter when persistent northeast winds (the prevailing winter winds) push Virginian coastal waters past Cape Hatteras and Diamond Shoals into Raleigh Bay and beyond (Bumpus and Pierce, 1955; Wells and Gray, 1960; Gray and Cerame-Vivas, 1963), creating favorable conditions for "northern" species to live in the Carolinian Province temporarily.

ABUNDANCE AND DISTRIBUTION

Although level bottoms of sand and mud predominate on the North Carolina shelf, scattered here and there are hard substrates: reefs of Trent Marl covered with calcareous tubes of mollusks, coquina formations, encrusted *Lithothamnion* algae, patches of coral, shelly areas, and wrecks that support a varied and abundant biota. The submerged reefs are well known to fishermen but, unfortunately, have been little studied by biologists. Pearse and Williams (1951) pioneered in describing the biota of the reefs off New River Inlet. More recently Menzies, Pilkey, Blackwelder, Dexter, Huling, and McCloskey (1966) made a comprehensive study of a *Lithothamnion* reef near the edge of the shelf off Onslow Bay. The fauna listed was predominantly tropical and subtropical. Pearse and Williams reported four sea-stars on their inshore reefs; Menzies et al. (1966) identified but one asteroid from their offshore reef. Granite substrates are limited to the inshore, shallow-water man-made jetties. Not all sea-stars require a hard substrate, but some that do (*Echinaster spinulosus* and *Thyrastra serpentarius*, for example) are not abundant elsewhere. Grass beds (principally eelgrass *Zostera* and widgeon grass *Ruppia*), limited to soft bottoms of the estuaries, may be ignored as habitats for starfishes, although occasionally the very young of *Asterias forbesii* are found here.

The 33 species of sea-stars definitely known to occur on the North Carolina Continental Shelf fall into 22 genera. Of the four genera that have

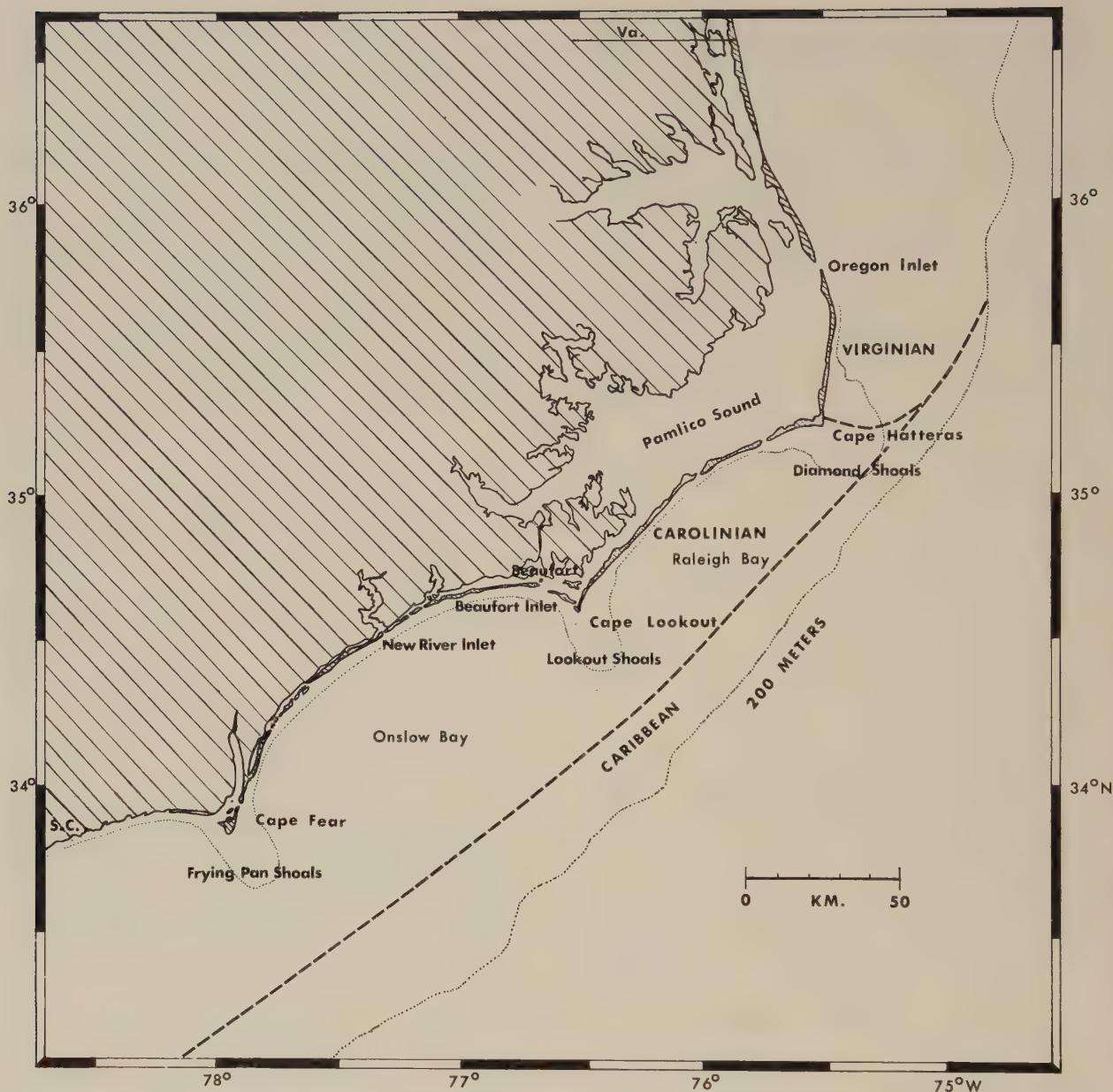


FIGURE 1.—Map of the North Carolina coast showing relation of the three major biotic provinces (Virginian, Carolinian, and Caribbean) to Cape Hatteras and the Continental Shelf. The heavy broken lines indicate the approximate boundaries between the provinces.

more than one species, three contain the four most common species. These are, in order of abundance: *Astropecten articulatus*, *Luidia clathrata*, *Astropecten americanus*, and *Asterias forbesii*. The first two occur in large numbers on level bottoms in 10 to 100 m. in Raleigh Bay and Onslow Bay, and commonly appear together in trawls of shrimp and scallop fishermen. Their numbers diminish north of Cape Hatteras and nearer the edge of the shelf.

Astropecten americanus, on the other hand, is abundant north of Cape Hatteras but is rare south of the cape. *Asterias forbesii*, a shallow-water species, is the only sea-star that lives permanently within the estuaries. At times it is very abundant on the jetties. *Astropecten articulatus* and *L. clathrata* are sometimes discarded in the estuaries by shrimp fishermen when they clean their nets and boats, but these species seem to be unable to survive

here throughout the year—perhaps from lack of suitable substrate on which to feed, or because of their inability to withstand winter cold or occasional lowered salinity in the shallow estuaries.

The starfishes of North Carolina predominantly have a southern affinity. Eighteen species range from North Carolina southward and nine from North Carolina northward. Only six are found

both north and south of North Carolina, and four of these are more southern than northern. One (*Coscinasterias*) extends only as far north as Virginia, and three as far as New Jersey. Comparison of figures 2 and 3 shows that strictly "northern" species—those that range northward from North Carolina—are rare south of Cape Hatteras. They appear in the cool south-flowing Virginian Coastal

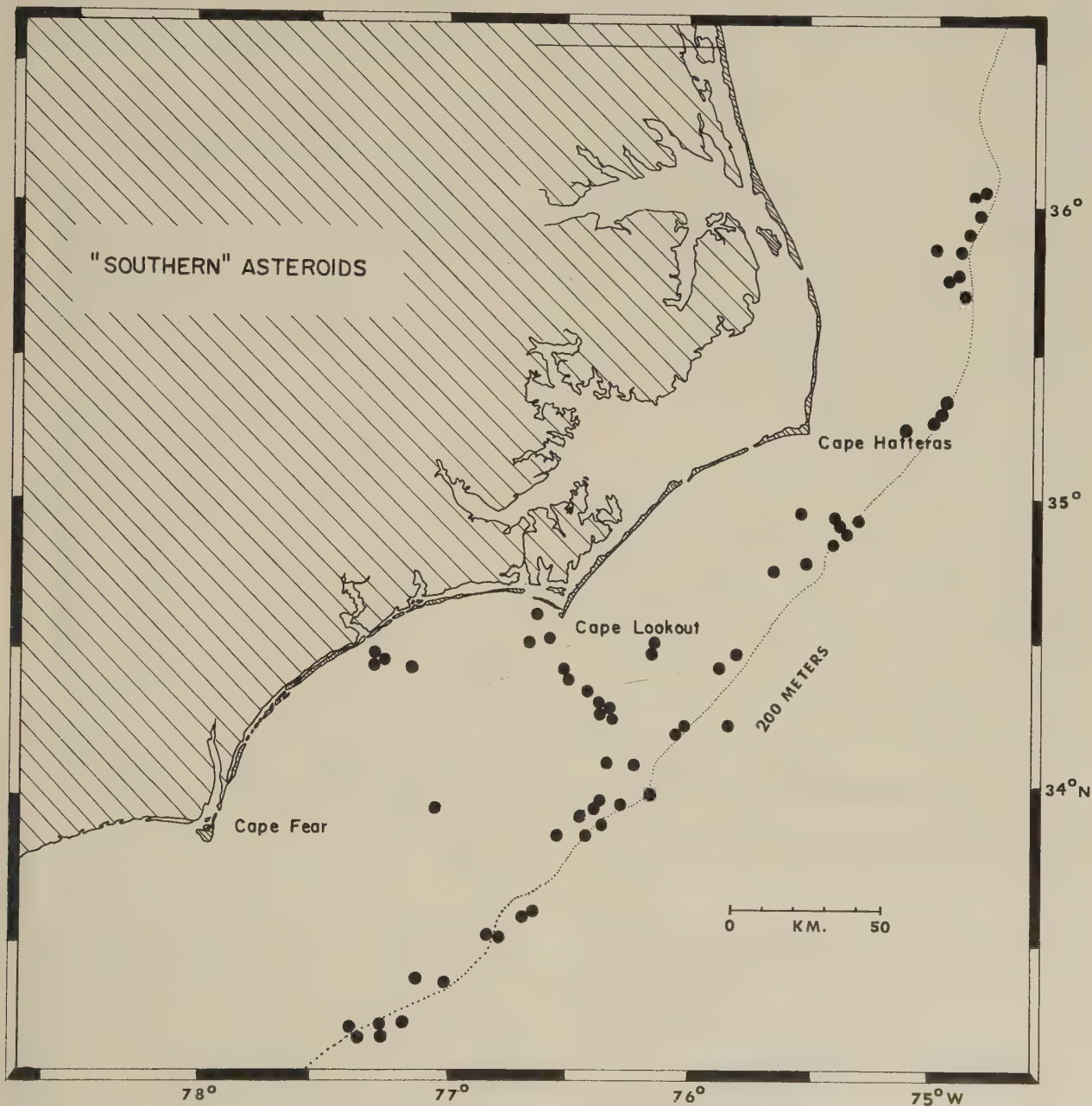


FIGURE 2.—Stations in North Carolina at which 16 of the 18 "southern" asteroids have been taken.

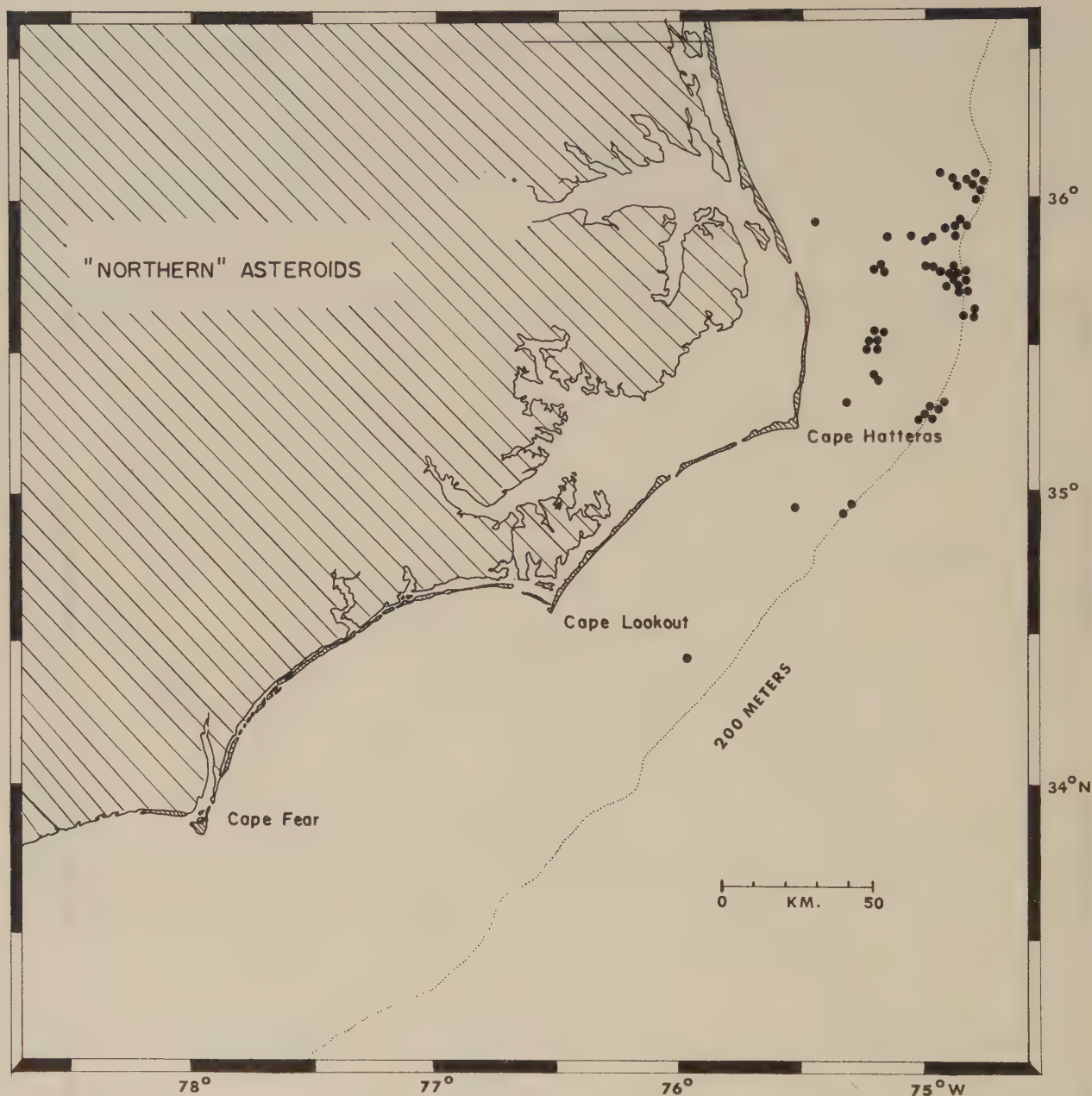


FIGURE 3.—Stations in North Carolina at which seven of the nine "northern" asteroids have been taken.

Current or in deeper waters near and off the edge of the shelf. On the other hand, "southern" species—those that are distributed from North Carolina southward—rarely are taken in stations north of Cape Hatteras except near the edge of the shelf under the Florida Current.

A greater number of species, but smaller populations, occur along the outer shelf (110–200 m.),

whether in the Caribbean Province or north of it, than in either the Virginian or Carolinian Province. Either or both of two factors not easily separated may account for this distribution: depth and more uniform temperature. The range of bottom temperatures of the outer shelf is far less than that of either the middle or inner shelf. North of lat. 35°30' N., northern and southern species ap-

pear to overlap somewhat. The few stations from which tropical species have been taken in this region may be under the Florida Current at some times but not at others, owing to the meanderings of the current. Also, the average bottom temperature is higher than it is nearer shore or in the deeper water of the slope.

Table 1 indicates the affinities of the various species in relation to their geographic ranges and to the biotic provinces of the shelf. The distribution of North Carolina asteroids largely follows the distribution pattern shown by Cerame-Vivas and Gray (1966) for other benthic species of the area.

TABLE 1.—*Asteroidea* known to occur in North Carolina waters, their geographic affinities, and areas of distribution on the Continental Shelf

Geographic affinity and species	Biotic Provinces		
	Virginian	Carolinian	Caribbean
Northern and Southern:			
<i>Coronaster briareus</i>	X		
<i>Odontaster hispidus</i>	X	X	
<i>Asterias forbesii</i>	X	X	
<i>Astropecten articulatus</i>	X	X	X
<i>Luidia clathrata</i>	X	X	X
<i>Tethyaster vestitus</i>			X
Northern:			
<i>Asterias vulgaris</i>	X		
<i>Ctenodiscus crispatus</i>	X		
<i>Henricia sanguinolenta</i>	X		
<i>Leptasterias tenera</i>	X		
<i>Pellaster planus</i>	X		
<i>Porania insignis</i>	X		
<i>Astropecten americanus</i>	X	X	X
<i>Asterias tanneri</i>	X		X
<i>Mediaster bairdii</i>			X
Southern:			
<i>Echinaster sentus</i>		X	
<i>Echinaster spinulosus</i>		X	
<i>Thyraster serpentarius</i>		X	
<i>Astropecten duplicatus</i>		X	X
<i>Coscinasterias tenuispina</i>		X	X
<i>Luidia alternata</i>		X	X
<i>Astropecten nitidus</i>			X
<i>Astropecten nuttingi</i>			X
<i>Echinaster brasiliensis</i>			X
<i>Goniaster americanus</i>			X
<i>Linckia bouvieri</i>			X
<i>Luidia bernasconiae</i>			X
<i>Luidia elegans</i>			X
<i>Narcissia trigonaria</i>			X
<i>Oreaster reticulatus</i>			X
<i>Plinthisaster denticatus</i>			X
<i>Solaster caribbaeus</i>			X
<i>Stephanasterias gracilis</i>			X

The entire benthic fauna is largely "southern," that is, more species range southward from North Carolina than range northward. Fourteen of the 33 asteroids, all tropical or subtropical, occur only in the Caribbean Province. No strictly tropical species gets into the Virginian Province. On the other hand, some of the northern species do find their way into the Carolinian Province and sometimes into the Caribbean Province, especially at its northern end. Only three starfishes were found in

all three biotic areas—but not in equal abundance in all of them. For example, *Luidia clathrata* and *Astropecten articulatus* are much more abundant in the Carolinian Province than in either the Virginian or Caribbean Province. The only "northern" species not collected in the Virginian Province is *Mediaster bairdii*. Thus far this species has been collected only from the edge of the shelf off Cape Lookout. Similarly, *Tethyaster*, a species that ranges both north and south of North Carolina, has been taken only in the Caribbean Province.

IDENTIFICATION OF SPECIES

Although the following keys cover the sea-stars now known to occur on the North Carolina shelf, it would not be surprising if additional species, especially Caribbean species, were collected from time to time. Technical terms are defined in the glossary and illustrated in figure 4. Additional details of morphology may be obtained from Hyman's (1955) volume on the Echinodermata, from which much of the terminology used here has been taken.

GLOSSARY

Abactinal: Upper or aboral surface opposite mouth and ambulacral grooves.

Aboral: See abactinal.

Actinal: Oral or lower surface on which mouth and ambulacral grooves are situated.

Adambulacrum: Ossicle in series bordering ambulacral groove adjacent to ambulacral ossicles.

Alveolar pedicellaria: Pedicellaria with two valves which are partly sunken into a depression on a plate.

Ambulacrum: Groove on the actinal surface of the arm, from mouth to arm tip, containing the tube feet. Also, a plate of the double series flooring the ambulacral groove.

Ampulla: Rounded (single) or bilobed (double) sac above each tube foot.

Bivalved pedicellaria: Pedicellaria having two valves.

Capitate: Enlarged at tip.

Carina: Distinct median row of plates on aboral surface of arm.

Clavate: Club-shaped.

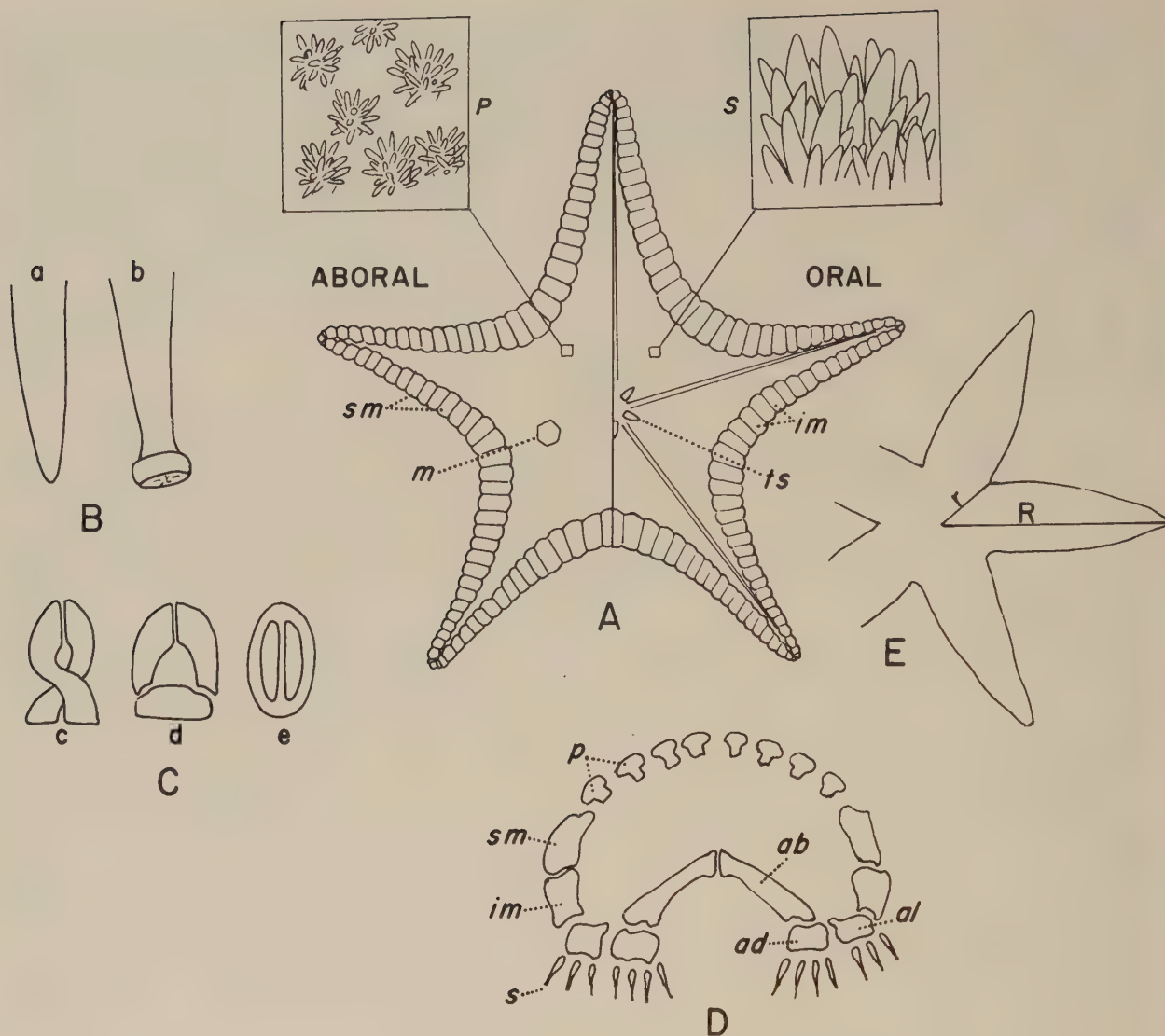


FIGURE 4.—Some morphological characteristics used in identification of asteroids (somewhat schematic). A. Aboral and oral sides of a starfish (*Odontaster hispidus*). B. Podia, without (a) and with (b) sucker. C. Pedicellaria, crossed (c); straight (d); and bivalve (e). D. Arm in cross section, showing ossicles. E. Radii. ab, ad, al—ambulacral, adambulacral, and actinolateral ossicles; im, inferomarginal plates; m, madreporite; p, paxillae; R, long radius; r, short radius; s, spines; sm, superomarginal plates; ts, tooth spine.

Cribriform organ: Vertical depression between adjacent marginals, lined with a series of thin vertical plates (lamellae).

Disc: Body of starfish, exclusive of arms.

Epiproctal cone: A sharp dermal elevation in the center of the aboral surface of certain starfish.

Fasciolated: Banded with small spinules, or ciliated.

Feliped pedicellaria: Straight pedicellaria with overlapping claws resembling a cat's forepaws when faced together.

Furrow: Groove running between adjacent series of plates.

Granule: Small grain.

Hyaline: Clear, glassy.

Imbricate: Overlapping.

Inferomarginal: Plate in lower marginal series.

Interradial: Between arms.

Lamella: Thin vertical platelet.

Lateral: Along sides, between actinal and abactinal.

Lateral furrow: Groove between superomarginals and inferomarginals.

Madreporite: Stony sieve-plate at terminus of water vascular system, on aboral surface, between margin and center of disc.

Mammilliform: Nipple-shaped.

Marginals: One or two series of plates bordering arms and disc, around periphery.

Mouth frame: Ossicles surrounding mouth opening.

Oral: Surface on which mouth is located.

Ossicle: Plate, or skeletal element.

Papilliform pedicellaria: Raised or elevated pedicellaria.

Papula: Thin respiratory evagination of the body wall which emerges between ossicles.

Papular pore: Pore through which papula projects.

Paxilla: Aboral plate drawn up into a column which is usually crowned with spinules.

Paxillate: Surface covered with paxillae.

Paxilliform: Shaped like a paxilla.

Pedicellaria: Small calcareous "pincher," of which there are various types, used mostly to remove particulate matter from surface of starfish.

Pentagonal: Five-sided, without distinction between disc and arms.

Podia: Tube feet.

Radial furrow: Furrow on actinal surface running from ambulacral groove to margin.

Radius: Long radius (R), distance from center of disc to tip of arm; short radius (r), radius of disc.

Reticulate: Netlike, a network.

Sessile pedicellaria: Pedicellaria resting directly on surface, not raised or sunken.

Spine: Sharp, calcareous projection resting on underlying plate.

Spinule: Very fine small spine.

Stellate: Radiating, starlike.

Sucker: Disc or flattened tip at end of tube foot.

Superomarginal: Plate of upper series of marginals.

Sutural groove: Groove between adjacent marginals.

Terete: Cylindrical, tapering.

Tessellate: Mosaic of small fairly regular plates.

Tridentate: With three teeth or valves.

Triseriate: In a series of three.

Tubercle: Calcareous projection shorter and thicker than spines.

Valvular pedicellaria: Pedicellaria with two valvelike pieces.

Wart: Calcareous projection larger than granule but smaller than tubercle.

KEY TO THE ORDERS OF NORTH CAROLINA ASTEROIDEA

- | | |
|--|-------------------|
| 1. Podia without suckers----- | 2 |
| Podia with suckers----- | 3 |
| 2. Superomarginals absent---- | Platyasterida (I) |
| Superomarginals present---- | Paxillosida (II) |
| 3. Marginals conspicuous----- | Valvatida (III) |
| Marginals inconspicuous or absent----- | 4 |
| 4. Pedicellariae absent----- | Spinulosida (IV) |
| Pedicellariae present----- | Forcipulatida (V) |

I. Key to the Species of Platyasterida

- | | |
|---|----------------------------|
| 1. Arms with wide transverse bands or blotches of black or brown-- | <i>Luidia alternata</i> |
| Arms without transverse color bands---- | 2 |
| 2. Inferomarginals with three spines, upper one much larger than others (young specimens may have only two) ----- | <i>Luidia elegans</i> |
| Inferomarginals with two spines----- | 3 |
| 3. Paxillae quadrangular, skeleton compact ----- | <i>Luidia clathrata</i> |
| Paxillae stellate, skeleton fragile ----- | <i>Luidia bernasconiae</i> |

II. Key to the Species of Paxillosida

- | | |
|--|------------------------------|
| 1. Superomarginals separated by gap----- | <i>Otenodiscus crispatus</i> |
| Superomarginals broadly in contact---- | 2 |
| 2. Marginal fringe of flattened, rectangular spines, usually not projecting much beyond margin; large size. <i>Tethyaster vestitus</i> | |
| Marginal fringe of acute spines forming conspicuous border; moderate size-- | 3 |
| 3. Rays long, slender; superomarginals small, numerous----- | 4 |
| Rays not very long, robust; superomarginals large, few----- | 5 |

4. Paxillar spinules long, slender, movable;
paxillae in irregular narrow transverse
rows ----- *Astropecten americanus*
Paxillar spinules small, clavate, fixed;
paxillae in regular wide transverse
rows ----- *Astropecten nuttingi*
5. All superomarginals without spines or
tubercles ----- *Astropecten nitidus*
Some superomarginals with spines or
tubercles ----- 6
6. Stout acute spine on at least two inter-
radial superomarginals.
Astropecten duplicatus
Small obtuse spine on distal half to three
quarters of superomarginals.
Astropecten articulatus

III. Key to the Species of Valvatida

1. Dorsal skeleton reticulate ----- 2
Dorsal skeleton tabulate or paxillate ---- 4
2. Disc large, arms short ---- *Oreaster reticulatus*
Disc small, arms long ----- 3
3. Arms triangular in cross section, taper-
ing to acute ends ----- *Narcissia trigonaria*
Arms cylindrical, with rather blunt
ends ----- *Linckia bouvieri*
4. Dorsal skeleton paxillate -- *Odontaster hispidus*
Dorsal skeleton tabulate ----- 5
5. Large heavy subacute spines on dorsal
surface ----- *Goniaster americanus*
No spines on dorsal surface ----- 6
6. Rr more than three to one; arms long,
acute ----- *Mediaster bairdii*
Rr less than two to one; arms short,
blunt ----- 7
7. Papulae few, in rows along each radius;
marginals covered with granules.
Plinthaster dentatus
Papulae numerous, scattered among
plates; marginals usually bare of
granules, at least in center -- *Peltaster planus*

IV. Key to the Species of Spinulosida

1. Arms five ----- 2
Arms six to eight ----- *Solaster caribbaeus*
2. Disc broad, with broadly based arms ----
Porania insignis
Disc small, with long, cylindrical arms -- 3

3. Dorsal and marginal plates quadrangu-
lar, overlapping at corners, in longi-
tudinal rows ----- *Thyraster serpentarius*
Dorsal and marginal plates not quad-
rangular, not overlapping at corners,
not in regular rows ----- 4
4. Small spines in groups or along ridges;
papulae on both surfaces -----
Henricia sanguinolenta
One or few coarse spines at nodes; no
papulae on oral surface ----- 5
5. Two adambulacral spines -----
Echinaster spinulosus
Three adambulacral spines ----- 6
6. Aboral spines in about five irregular
rows ----- *Echinaster sentus*
Aboral spines in 9 to 11 rows -----
Echinaster brasiliensis

V. Key to the Species of Forcipulatida

1. Aboral surface with short blunt spines
(tubercles) ----- 2
Aboral surface with slender spines, at
least along margins ----- 3
2. Arms somewhat flattened, sharply taper-
ing, with distinct median row of
aboral plates ----- *Asterias vulgaris*
Arms inflated, blunt at tip, no distinct
median row of aboral plates *Asterias forbesii*
3. Aboral spines with dense wreath of small
pedicellariae ----- 4
Aboral spines without dense wreath of
small pedicellariae ----- 5
4. With five arms ----- *Asterias tanneri*
With ten to twelve arms -- *Coronaster briarius*
5. Aboral plates arranged in definite rows,
one spine to each plate -----
Coscinasterias tenuispina
Aboral plates not arranged in definite
rows, more than one spine to each plate 6
6. Aboral surface with minute spines;
arms seven to nine -- *Stephanasterias gracilis*
Aboral surface with conspicuous spines;
arms five ----- *Leptasterias tenera*

DESCRIPTION OF SPECIES

The following descriptions are given merely as supplements to the keys and additional aids to identification. It is not the purpose of this paper to give a complete systematic treatment of the North Carolina species of Asteroidea, and diag-

noses and descriptions of higher taxa have, therefore, not been included. The species descriptions have been kept as simple as possible for quick identification.

The preceding keys are strictly artificial, and their usefulness is, therefore, limited to the Continental Shelf off North Carolina.

PLATYASTERIDA

In North Carolina the Order Platyasterida is represented by one genus and four species. Three species have "southern" affinity and are not abundant. Distribution of *Luidia clathrata* is far wider than that of other species in this genus (fig. 5).



FIGURE 5.—Distribution and relative abundance of four species of *Luidia*. Many of the numerous stations at which *L. clathrata* was collected have been omitted.

***Luidia alternata* (Say)**

Synonymy:

Asterias alternata Say, 1825.

Luidia alternata: Lütken, 1859.

Luidia variegata Perrier, 1876.

Description:

Rays five, long and fragile. Aboral paxillae with 10 to 16 slender, acute spinules surrounding stouter central 1 or 2; some paxillae much

larger than others, with large central spine, especially along margins of arms, and scattered on disc. Two to four lateral rows of paxillae larger than those on median portion of arm. Inferomarginals with two long acute upper spines and about three long spines and many small acute ones on lower side. Adambulacral with three or four spines. $Rr=8:1$. Color gray or light brown with broad irregular bands of black or dark brown across arms; tube feet frequently bright orange.

Range:

Southeast coast of the United States to Brazil, 10 to 200 m. Although not abundant, *L. alternata* is occasionally taken in dredges and trawls. Pearse and Williams (1951) reported it in North Carolina waters from reefs off New River Inlet.

***Luidia bernasconiae* A. H. Clark, 1945**

Description:

Rays five, very long and narrow. Adambulacral spines two, inner one flattened laterally, recurved. One or two large, acute or subacute spines on outer rows of dorsal paxillae, colored brown and white. Two large, less acute white spines on inferomarginals; many small sharp spines on marginals and in grooves between marginals. Paxillae in center of rays crowded, irregular, small; single outer row of paxillae dark, next two rows large, light, often forming distinct band down each side of arm. These three rows of paxillae may bear short, stumpy tridentate sessile pedicellariae, and some bear a large central spine. Paxillae with 5 to 10 clavate spinules surrounding central paxillar boss with larger, thicker spinule. Large tridentate pedicellariae on columnar interactinals, between adambulacral and inferomarginals, especially proximally (none distally). Marginal spines are long and erect, giving a thorny appearance. $Rr=7:1$. Color dark gray or brown above, white below.

Range:

Previously recorded only off Georgia (Clark, 1945). In North Carolina it has been taken several times, in depths of 20 to 110 m.

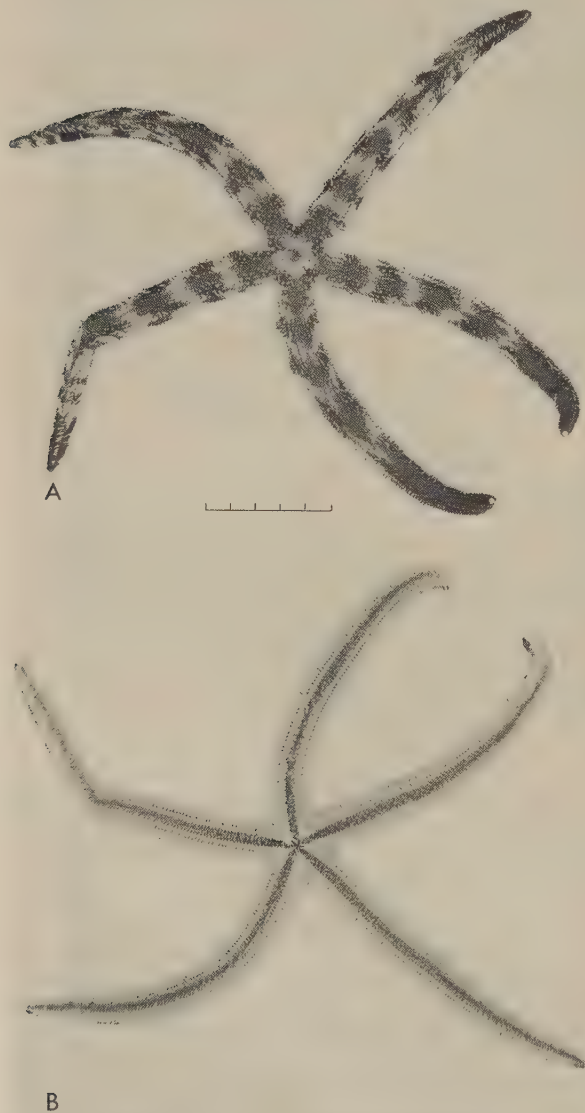
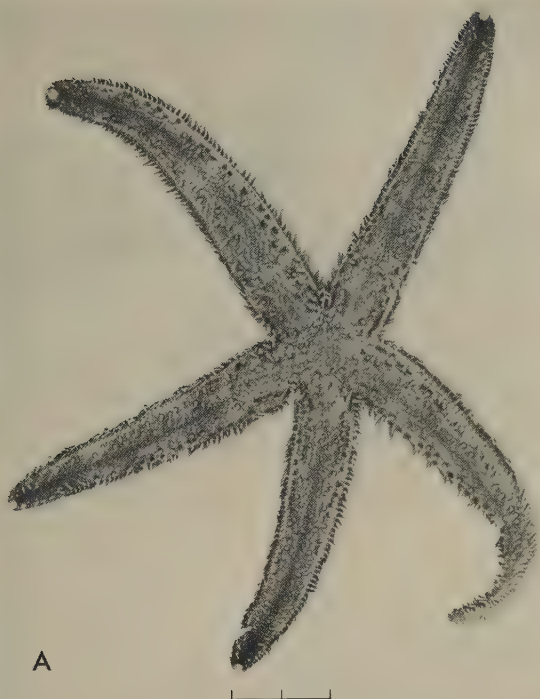
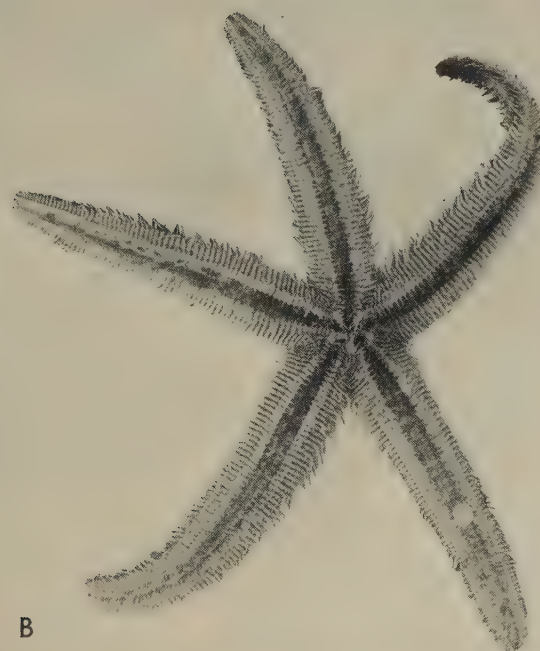


FIGURE 6.—*Luidia alternata*. A, aboral; B, oral. 5 cm. indicated.



A



B

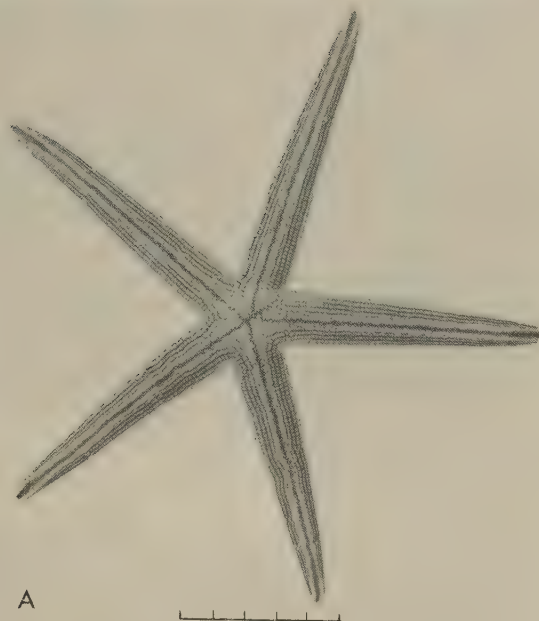
FIGURE 7.—*Luidia bernasconiae*. A, aboral; B, oral. 2 cm. indicated.

***Luidia clathrata* (Say)**

Synonymy:

Asterias clathrata Say, 1825.

Luidia clathrata: Lütken, 1859.



A



B

FIGURE 8.—*Luidia clathrata*. A, aboral; B, oral. 5 cm. indicated.

Description:

Rays five, long, straplike. Aboral surface flattened, regularly tessellated; paxillae quadrangular, 10 to 12 close, fairly regular rows, lateral rows distinctly larger than median rows. Paxillae covered with numerous short, coarse spinules. Inferomarginals with two

acute spines around bases. $Rr=6:1$. Color commonly gray or blue-gray, but may be salmon, rose, or light brown.

Range:

New Jersey to Brazil, 10 to 175 m. This species is the most common member of the genus in North Carolina and apparently the only one that is found north of Cape Hatteras. South of Cape Hatteras it is second only to *Astropecten articulatus* in abundance and is often taken with *Astropecten*. It is found in all three biotic provinces and in depths to 175 m., but is most abundant in the Carolinian Province in depths of 9 to 110 m.

***Luidia elegans* Perrier, 1876**

Description:

Rays five; aboral paxillae stellate, crowded, smallest in median portion of rays, larger near margins, with short central spinule and 6 to 10 marginal spinules not or scarcely enlarged at tip, giving very uniform appearance to paxillar area. Inferomarginals with two to three (three in fully grown specimens) large spines. Bivalved pedicellariae often present on actinal side. $Rr=7:1$. Color orange above, lighter below.

Range:

Cape Hatteras to Barbados, 95 to 267 m. Not common in North Carolina.

PAXILLOSIDA

In North Carolina, *Astropecten*, with five species, is the most conspicuous of the three genera in the Order Paxillosida. *A. articulatus* and *A. americanus* are the most abundant species. The relative abundance and distribution of the various species of *Astropecten* are indicated in figure 10. Although *A. americanus* and *A. articulatus* are very abundant, they apparently are not competitors for the same space. The former occurs mainly in the deeper waters of the shelf north of Cape Hatteras, and the latter is most abundant south of the Cape. The two species have not been taken in the same dredge haul. *A. duplicatus* has occasionally been found at the same station with *A. articulatus*, however, and *A. nitidus* and *A. nuttingi* have been taken together near the edge of the shelf east of Frying Pan Shoals.

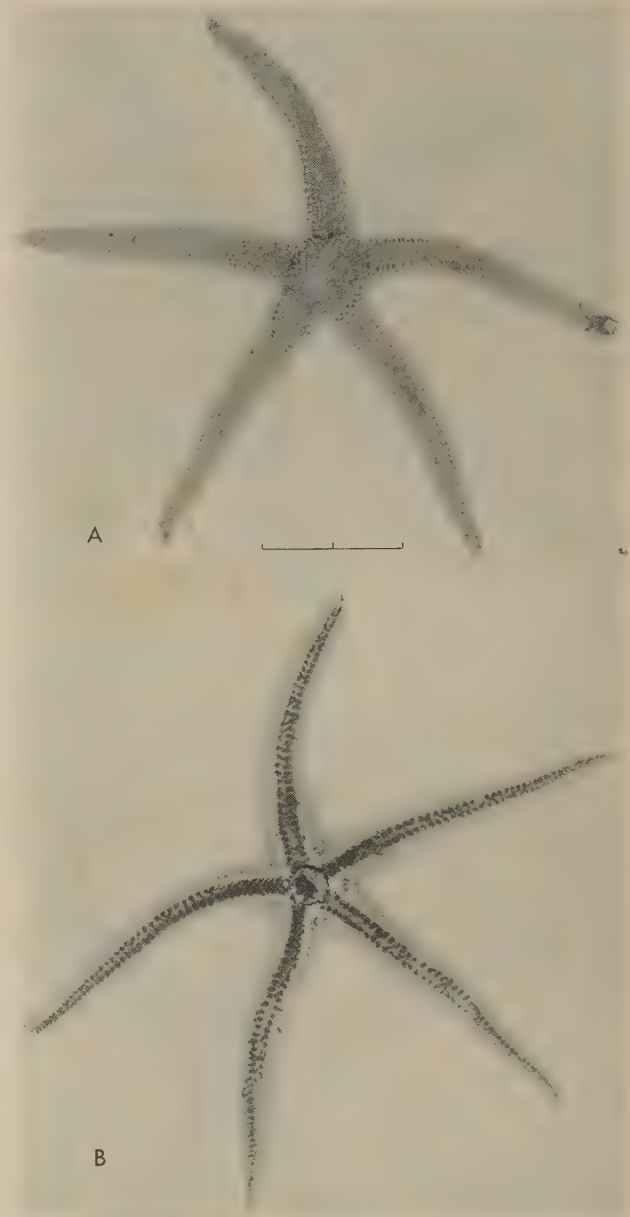


FIGURE 9.—*Luidia elegans*. A, aboral; B, oral. 2 cm. indicated.

***Ctenodiscus crispatus* (Retzius)**

Synonymy:

Asterias crispata Retzius, 1805.

Ctenodiscus crispatus: Duben and Koren, 1846.

Ctenodiscus australis Lütken, 1871.

Ctenodiscus krausei Ludwig, 1886.

Ctenodiscus procurator Sladen, 1889.

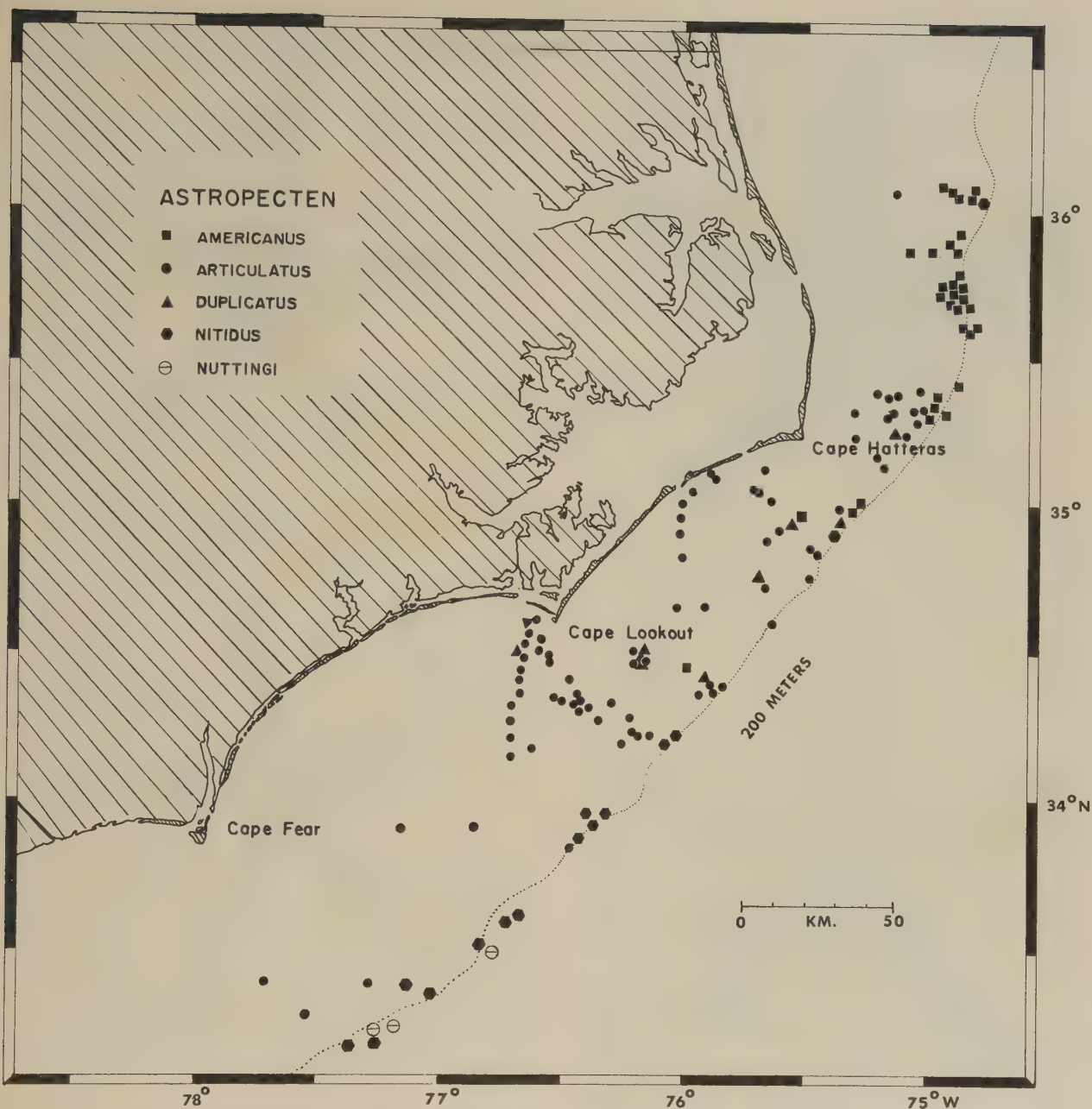


FIGURE 10.—Distribution and relative abundance of five species of *Astropecten*. Many of the numerous stations at which *A. articulatus* was collected have been omitted.

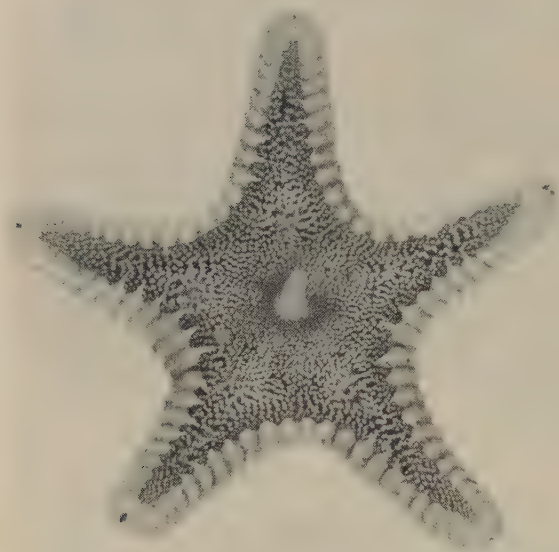
Description:

Five arms; body form variable, from almost pentagonal to nearly star-shaped. Aboral surface of typical paxillae; podia devoid of suckers. Conspicuous marginal plates, between each pair of which are simplified cribriform organs each in the form of a groove containing a few lamellae, which continue as simple

channels between plates of oral side up to ambulacral grooves. Lacks intestine, intestinal caeca, and anus. Epiproctal cone present. $Rr=1.6-3.1:1$. Color yellowish.

Range:

Circumboreal; in the Pacific, extends down to Chile; 55 to 1,800 m. Rare in North Carolina.



A



B

FIGURE 11.—*Ctenodiscus crispatus*. A, aboral; B, oral. 1 cm. indicated.

***Tethyaster vestitus* (Say)**

Synonymy:

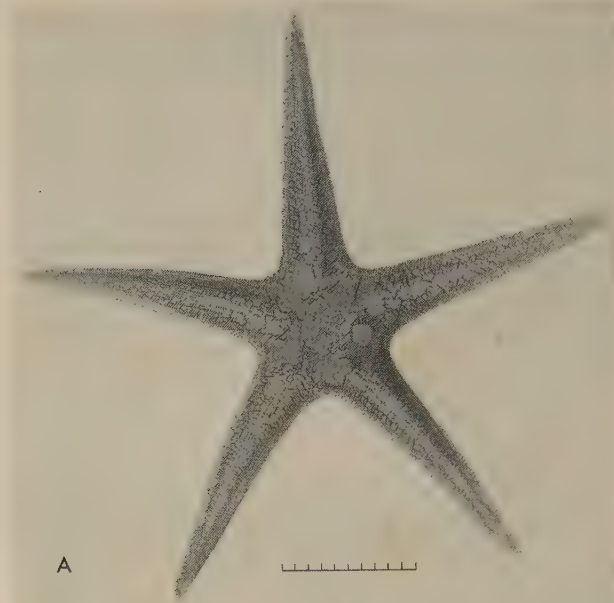
Asterias vestita Say, 1825.

Astropecten vestitus: Lütken, 1859.

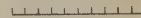
Sideriaster (?) *vestitus*: Verrill, 1914.

Description:

Form broadly stellate, with very large disc.
Arms five. Aboral surface closely covered with



A



B

FIGURE 12.—*Tethyaster vestitus*. A, aboral; B, oral. 10 cm. indicated.

uniform stellate paxillae. Upper marginals granulated, small, entirely lateral. Aboral interradial areas large, with numerous granulated plates. Madreporite very large, round, flat. Papular pores over entire aboral surface, about six around each plate. Adambulacrals with large median compressed spine, with two to three erect flattened spines on each side of furrow series; stout spines on actinal side,

with single or double row of shorter flat spines behind it. $Rr=4:1$. Color bright red or orange.

Range:

New Jersey to Venezuela, 37 to 293 m. North Carolina specimens were taken near the outer edge of the shelf.

***Astropecten americanus* Verrill**

Synonymy:

Archaster americanus Verrill, 1880.

Astropecten americanus: Verrell, 1894.

Description:

Body flat and thin; rays long, slender, tapering to acute tips. Aboral paxillar area about four times as wide as adjacent margin at base of ray. Paxillae small, with 6 to 10 elongate slender spinules surrounding central 1 or 2, in narrow transverse rows, rather openly spaced, so that papular pores are visible. Superomarginals small, numerous, usually broader than long, with deep, wide fasciolated grooves between; plates flat or concave. Inferomarginals project slightly beyond superomarginals, bear two slender, flattened, acute spines and sometimes a small papilliform pedicellaria; underside with small acute spines and spinules. Adambulacrals with three to five slender furrow spines. $Rr=5.5:1$. Color dark red or reddish brown.

Range:

East coast of the United States, 55 to 540 m. In North Carolina, *A. americanus* is limited largely to deeper waters of the outer edge of the shelf north of Cape Hatteras, where it appears to be the dominant asteroid. Bottom photographs show it to be abundant (fig. 14). Relatively few have been taken south of Cape Hatteras, where *A. articulatus* is the dominant *Astropecten*.

***Astropecten articulatus* (Say)**

Synonymy:

Asterias articulatus Say, 1825.

Astropecten articulatus: Mueller and Tro-schel, 1842.

Description:

Thick disc, five robust arms, with large stout superomarginals densely granulated. On distal half to three-quarters of rays, superomarginals sometimes bear a single small, obtuse spine on outer convex surface. Inferomargin-

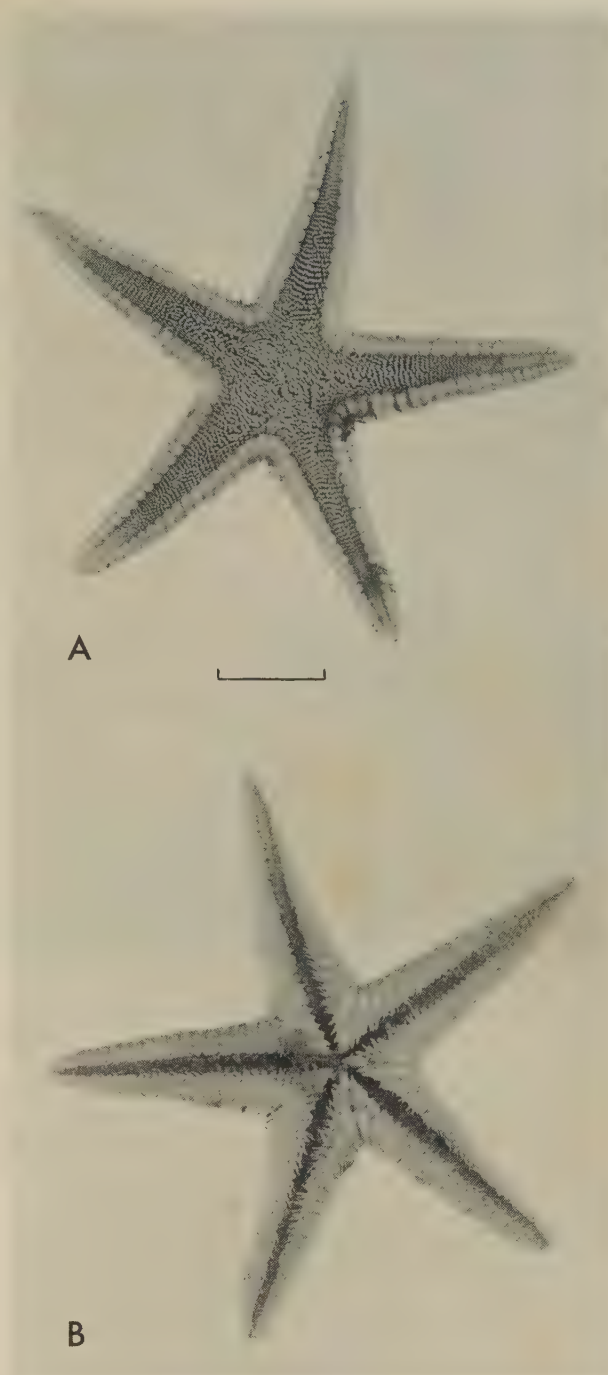


FIGURE 13.—*Astropecten americanus*. A, aboral; B, oral. 1 cm. indicated.

als with two short, flattened marginal spines, side by side. Adambulacrals triseriate. Aboral paxillae stellate, crowded, with six to eight short clavate spinules surrounding central one



FIGURE 14.—Photograph of sea floor showing abundance of *Astropecten americanus* at 165 m., northeast of Cape Hatteras. The area shown is about 4 m.²

to two. $Rr=4-6.5:1$. Color of paxillar area blue or purple, marginals white to orange.

Range:

New Jersey to Uruguay, 9 to 165 m. This is probably the most common sea-star in North Carolina, especially in Onslow and Raleigh Bays. Its abundance decreases north of Cape Hatteras. Trawlers take it in large numbers, frequently with *Luidia clathrata*. Although often found near the outer edge of the shelf, it is much more abundant in 18 to 110 m., where it glides over the sandy substrate and feeds on the numerous small organisms that abound there. Wells and Gray (1961) reported 93 species of small mollusks from the stomachs of 125 *A. articulatus*.

***Astropecten duplicatus* Gray**

Synonymy:

Astropecten duplicatus Gray, 1840.

Astropecten valenciennii Mueller and Tro-schel, 1842.

Astropecten variabilis Lütken, 1859.

Description:

Form stellate; rays five, angular, regularly tapered to narrow tips, high on sides at base. Superomarginals form thick border, elevated above paxillar area, with stout spine on first seven plates of each arm; spines on first two plates are largest. Inferomarginals project beyond superomarginals, forming lateral furrow felted with fine spinules. Surface of marginals granular. Inferomarginals with two to

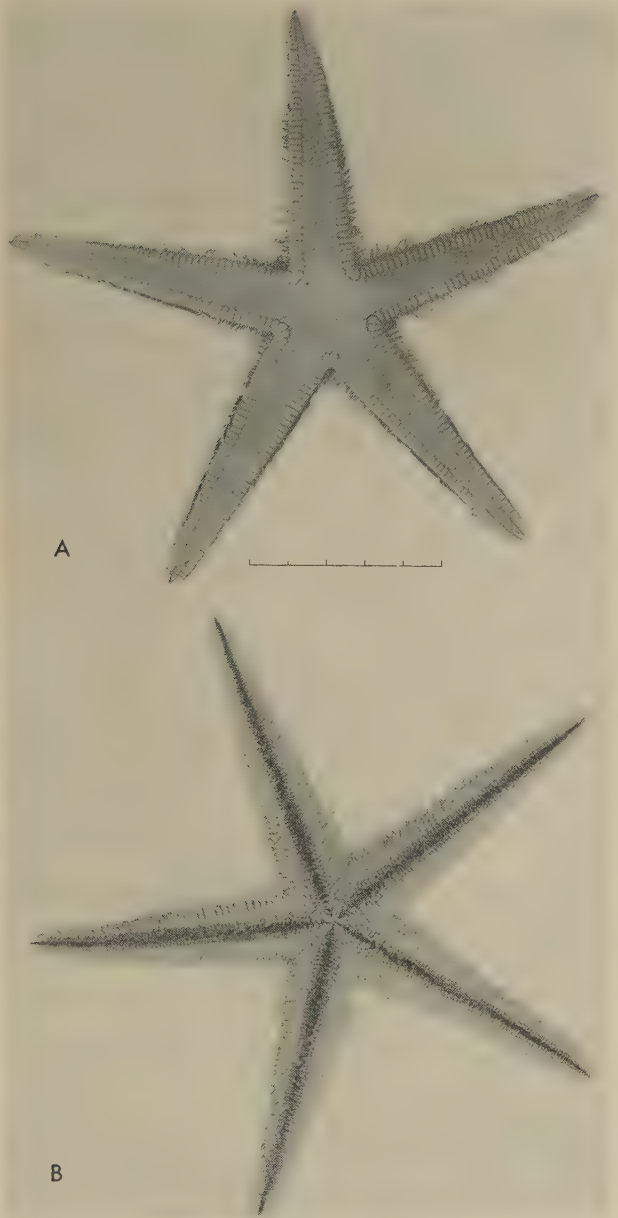


FIGURE 15.—*Astropecten articulatus*. A, aboral; B, oral. 5 cm. indicated.

three short, flattened, subacute spines. Aboral paxillae with 8 to 10 long clavate or capitate spinules surrounding 1 to 3 central ones. At base of rays, paxillae may have 12 to 16 spinules surrounding 4 to 8 central ones. Paxillae of generally uniform size and irregular arrangement. $Rr=5.3:1$. Color reddish brown or gray.

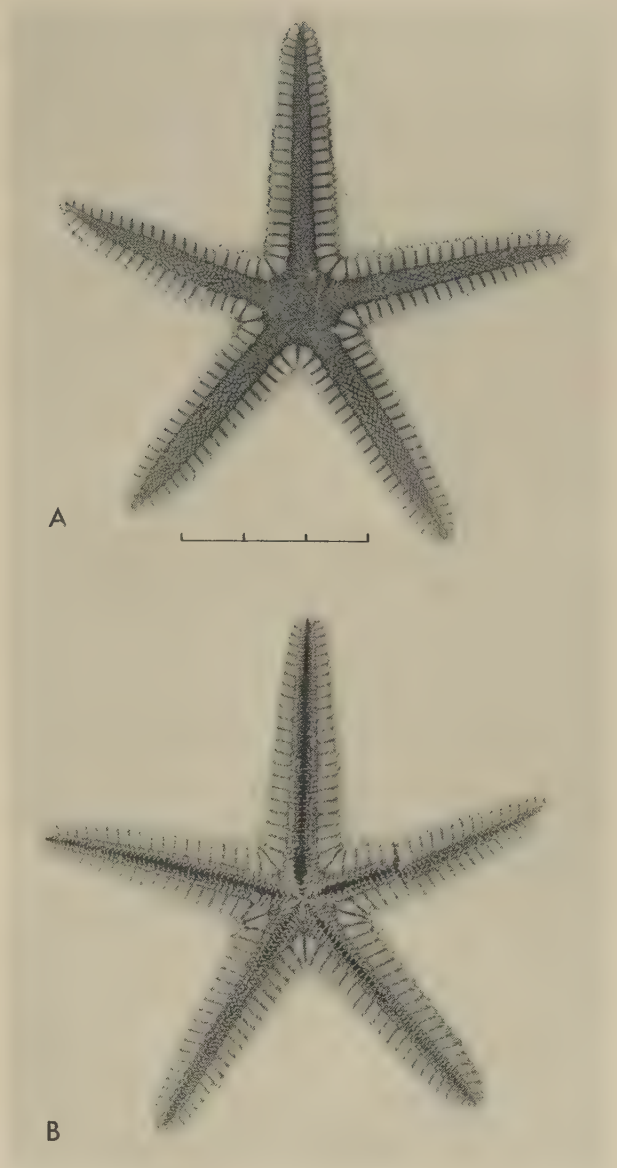


FIGURE 16.—*Astropecten duplicatus*. A, aboral; B, oral. 3 cm. indicated.

Range:

North Carolina to Brazil, 5 to 185 m. Although much less abundant, this species is sometimes collected with *A. articulatus*. It occurs mainly south of Cape Hatteras.

Astropecten nitidus Verrill, 1915

Description:

Body thick, stellate, with five short, acute rays. Superomarginals wide, convex, with deep transverse sutural grooves forming wide

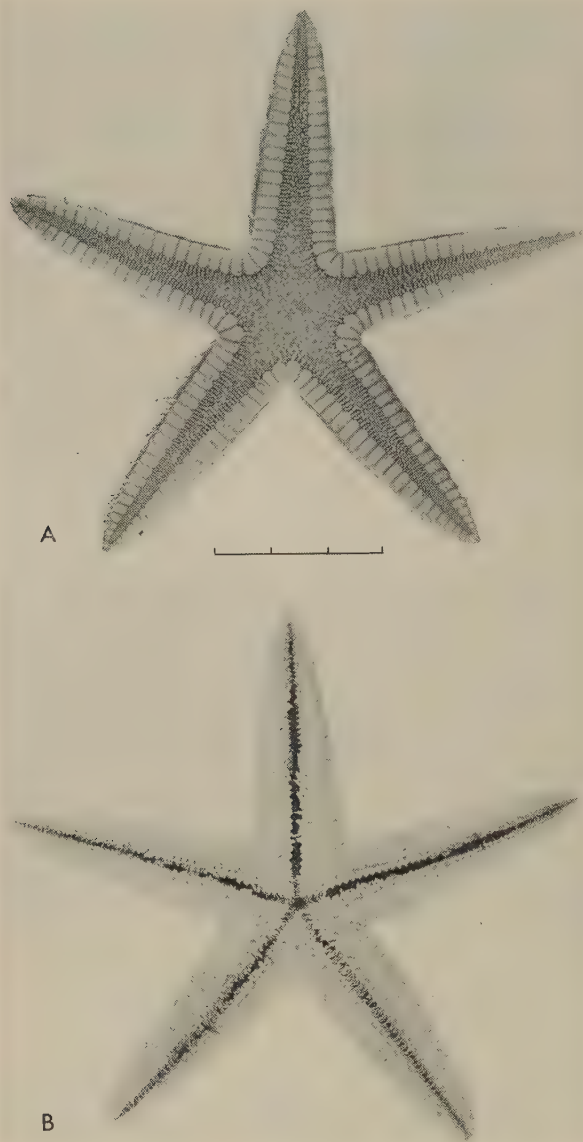


FIGURE 17.—*Astropecten nitidus*. A, aboral; B, oral. 3 cm. indicated.

prominent border, without spines or spinules, covered with granules. Aboral paxillar area narrow, less than twice width of adjacent marginals. Paxillae not very small, with 10 to 15 small, stellate, clavate spinules surrounding 1 to 2 central ones. Inferomarginals with two long, tapered, acute marginal spines, numerous fine, acute spinules, and two transverse rows of small acute spines on underside. $Rr=3.7:1$. Color light brown or cream, with blotches of rose pink.

Range:

North Carolina to Florida, 50 to 225 m. In North Carolina this species appears to be limited to the edge of the shelf, in 145 to 210 m. It is apparently more abundant between Cape Lookout and Cape Fear than between Cape Lookout and Cape Hatteras.

Astropecten nuttingi Verrill, 1915

Description:

Rays five, shape regularly stellate, flat and thin. Epiproctal cone usually prominent. Marginals small, covered with tiny, fine spinules; may bear a short, tapered spine on upper side of superomarginal. Inferomarginals reach to adambulacrals and are covered with small acute spines, with two to three long somewhat compressed marginal fringe spines. Paxillae small, equal, even, arranged in obliquely transverse rows, with 0 to 10 short slender spinules around crown and 1 to 2 in center of crown. Adambulacrals with marginal row of three slender spines, central one slightly curved and compressed. Madreporite small, usually concealed by paxillae. $Rr=5:1$. Color reddish, with deep red median line on each arm.

Range:

North Carolina to Florida and the Bahamas, 165 to 412 m. Although the least abundant of the North Carolina *Astropectens*, it is not uncommon along the 180- to 200-m. contour east of Cape Fear.

VALVATIDA

None of the species in this group can be considered common in North Carolina. Some are taken only rarely.

Oreaster reticulatus (Linnaeus)

Synonymy:

Asterias reticulatus Linnaeus, 1758.

Oreaster reticulatus: Mueller and Troschel, 1842.

Pentaceros reticulatus Agassiz, 1877.

Description:

Large, heavy stellate form, disc arched, inflated; arms four to six (normally five), short, acute. Skeleton reticulate, plates bar-shaped, with short, stout, conical spine at nodes. Marginals granular, covered with skin, each with a large conical spine. Papular areas conspicu-

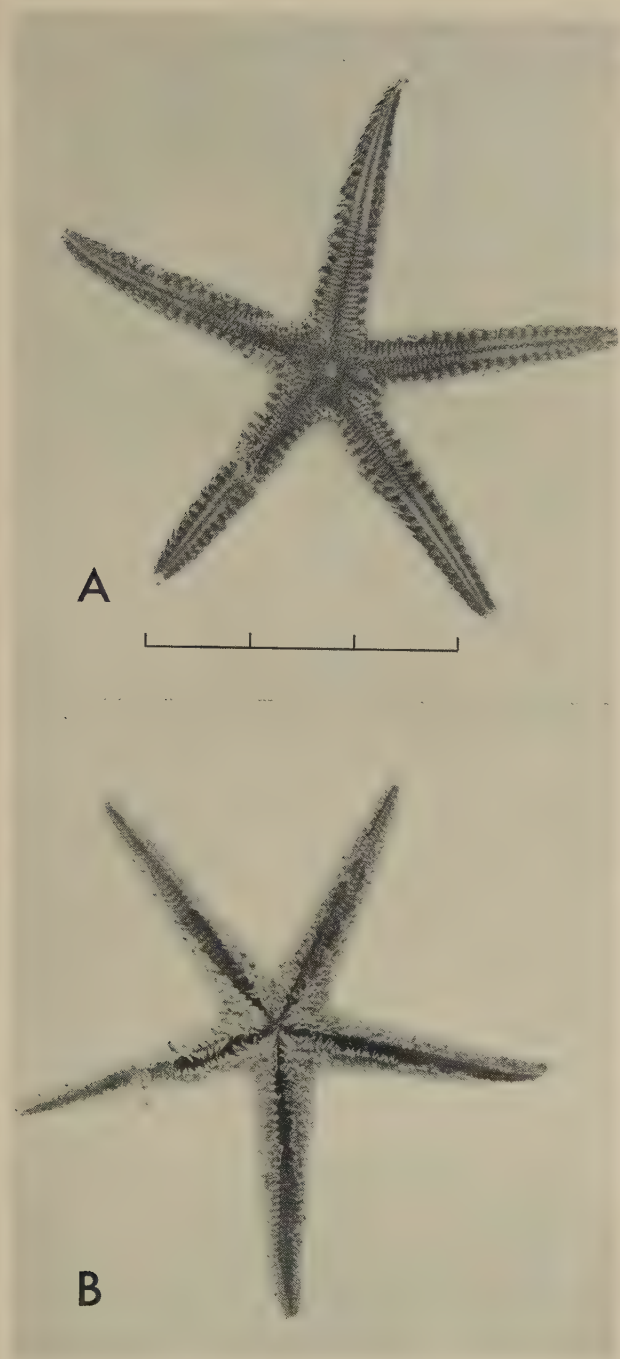


FIGURE 18.—*Astropecten nuttingi*. A, aboral; B, oral. 3 cm. indicated.

ous. Aboral surface covered by thick mosaic of plates with short stout central spine. Bivalved pedicellariae present. $Rr=2:1$. Color reddish brown, deep olive green, or yellowish orange.

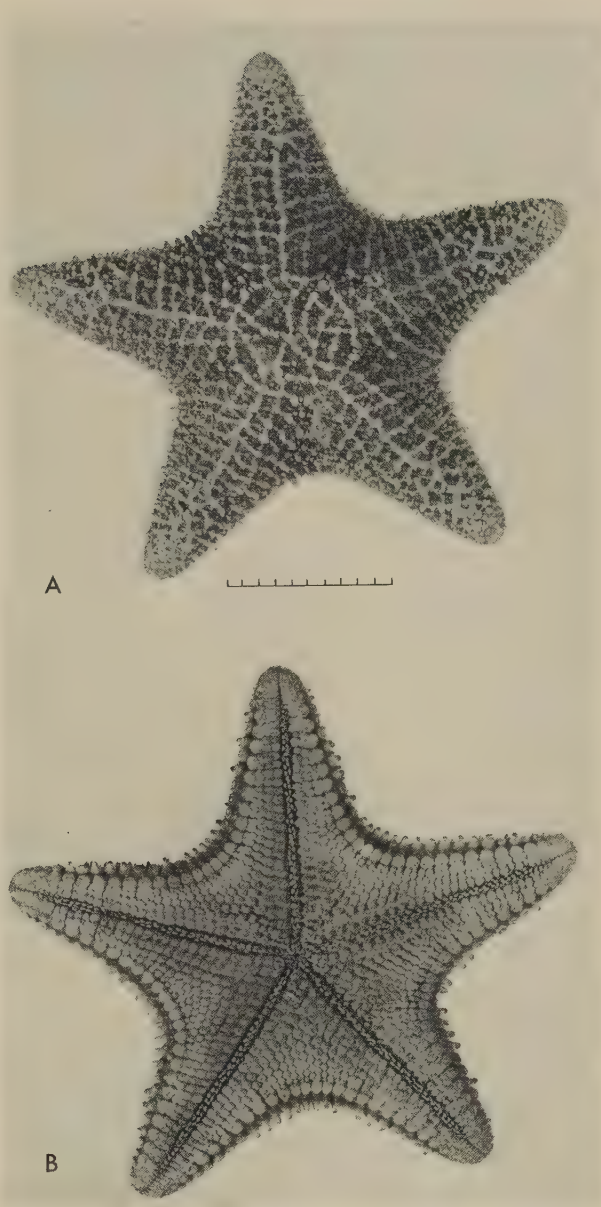


FIGURE 19.—*Oreaster reticulatus*. A, aboral; B, oral. 10 cm. indicated.

Range:

North Carolina to Brazil; Cape Verde Islands. Shallow water. A tropical species taken only rarely in North Carolina.

Narcissia trigonaria Sladen, 1889

Description:

Rays five, elongate, tapering to sharp end, triangular in cross section, with distinct median keel. Marginal plates well defined. Disc small,

Range:

North Carolina to Gulf of Mexico. A single specimen taken at the edge of the shelf off Cape Lookout in 210 m. constitutes a new record for North Carolina.

Linckia bouvieri Perrier, 1875

Description:

Disc small, rays five, long, slender, rounded. Primary plates of aboral surface large, irregular, rounded, tumid, five or more on disc. Plates become smaller, more numerous, and crowded distally. Papulae numerous, in clusters confined to aboral surface. Interactinal plates in two or more close rows. Inner adambulacral spines a close row of broad, somewhat flattened spines alternating with much smaller blunt, peglike spines; outer row of larger, stouter, more rounded spines arranged behind each small inner spine. Entire actinal and abactinal surface covered with fine granules. $Rr=10:1$. Color reddish fawn, primary plates and oral surface cream.

Range:

North Carolina to the West Indies, 73 to 360 m. Taken from near the edge of the shelf off Cape Lookout.

Odontaster hispidus Verrill, 1880

Description:

Form depressed, stellate, with broad disc. Rays five. Single, hyaline, recurved spine at apex of each jaw. Marginals only moderately developed, convex, separated by wide sutural grooves. Aboral plates elevated, capitate, with dense cluster of slender, elongate spinules. Interactinals (between adambulacrals and marginals) with stout, elongate, acute or subacute spinules. Large papular pores over most of radial areas and center of disc. $Rr=2.2:1$. Color pale salmon or yellowish.

Range:

Cape Cod to Florida, 30 to 875 m. Most of the stations from which this species has been taken are north of Cape Hatteras.

Goniaster americanus Verrill

Synonymy:

Goniaster americanus Verrill, 1871.

Pentagonaster semilunatus Perrier, 1876.

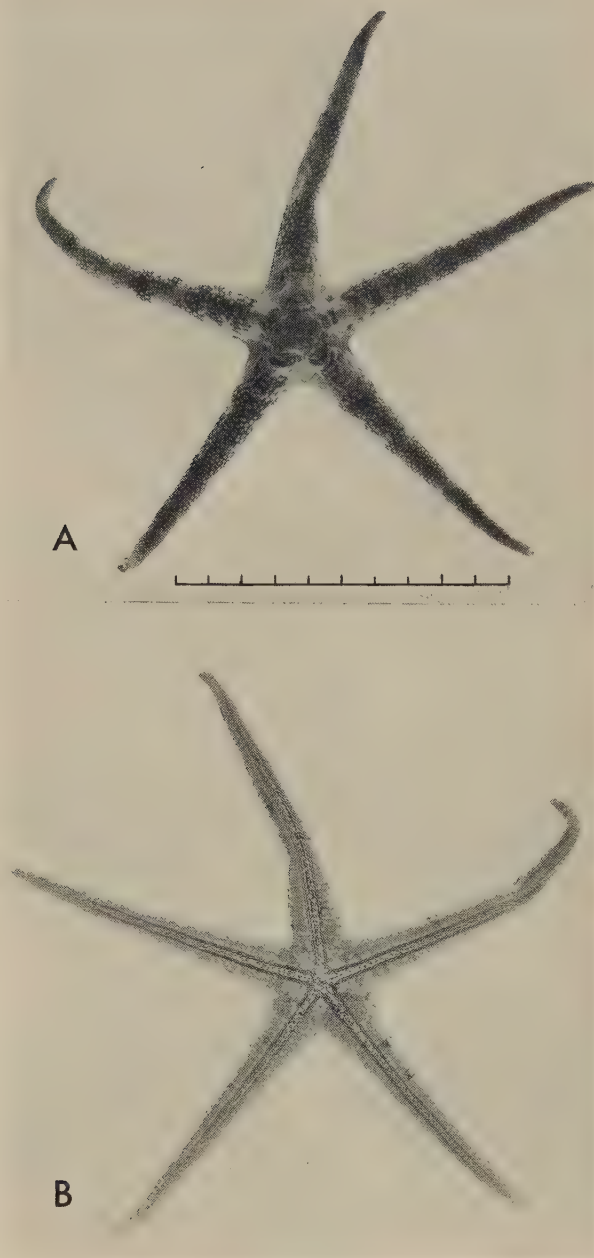


FIGURE 20.—*Narcissia trigonaria*. A, aboral; B, oral. 10 cm. indicated.

elevated. All plates covered with minute, uniform granules. Papulae single. Adambulacral spines in three series, broader at tip than at base, rather chisel shaped. Madreporite small, striated. $Rr=6.7:1$. Color creamy yellow with blotches of rusty red.

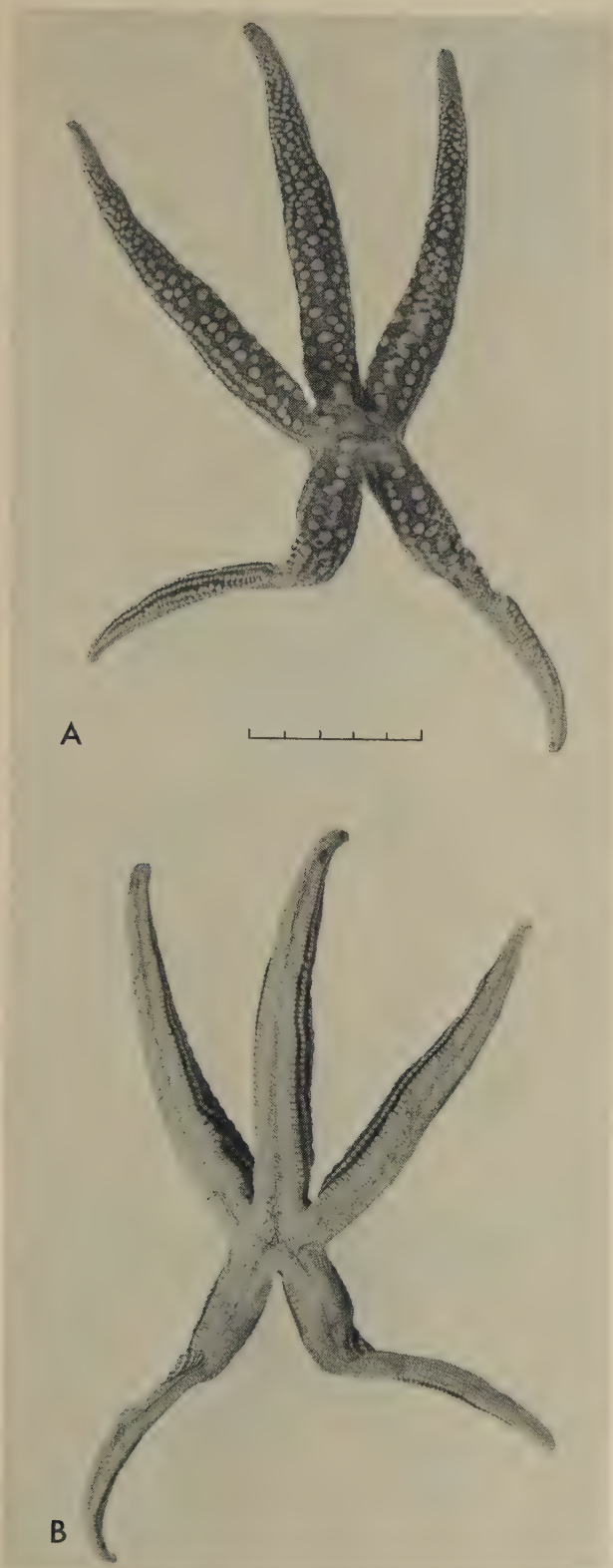


FIGURE 21.—*Linckia bouvieri*. A, aboral; B, oral. 5 cm. indicated.

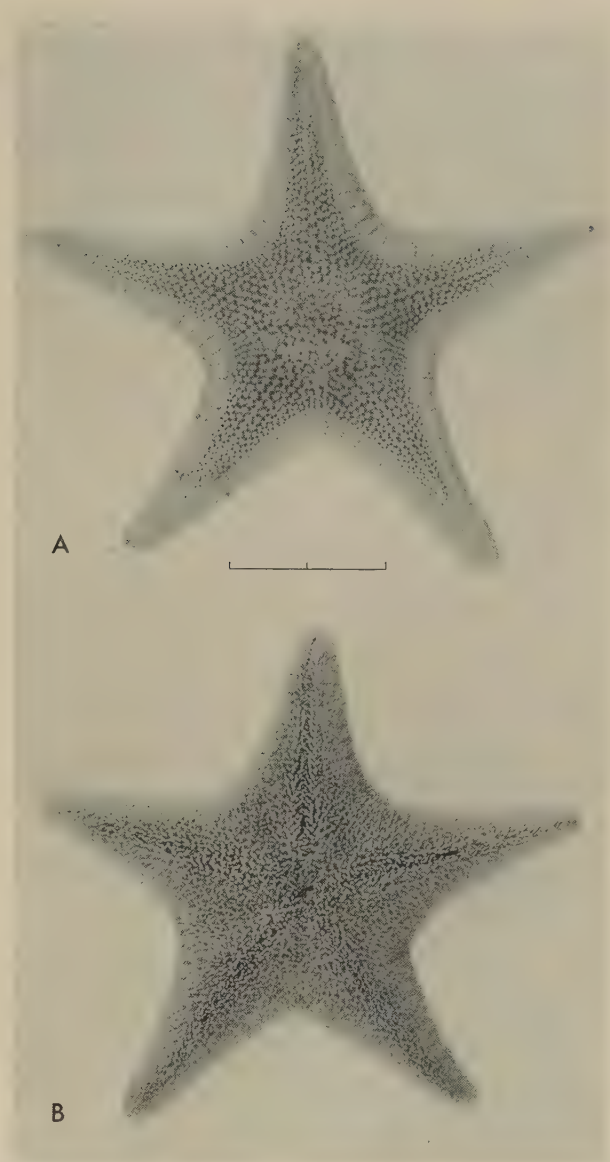


FIGURE 22.—*Odontaster hispidus*. A, aboral; B, oral. 2 cm. indicated.

Pentagonaster parvus Perrier, 1883.

Phaneraster semilunatus: Perrier, 1894.

Description:

Broadly pentagonal, with concave sides and short rays. Aboral plates large, polygonal or circular, covered with granules, many with a large, conical spine. Supermarginals and inferomarginals about equal, large, convex, quadrangular, with rounded inner sides, six to nine on each side of ray (number depends on age). Numerous alveolar pedicellariae with spatulate blades on oral and aboral surfaces,

Mediaster bairdii Verrill

Synonymy:

Archaster bairdii Verrill, 1882.

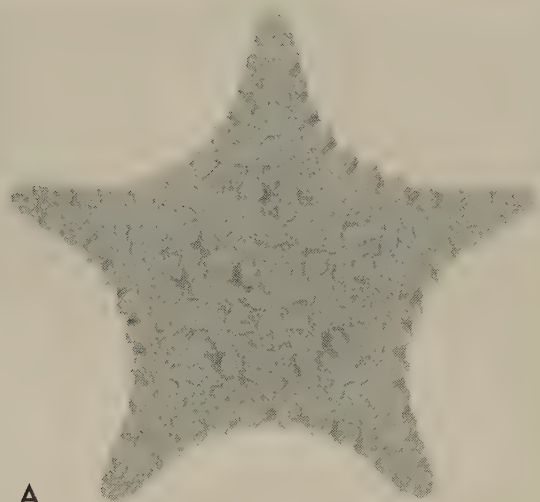
Mediaster stellatus Perrier, 1891.

Isaster bairdii: Verrill, 1895.

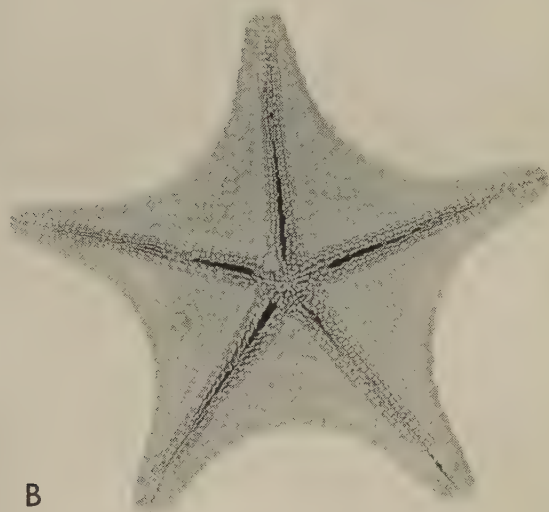
Mediaster bairdii: Verrill, 1899.

Description:

Form stellate, with broad flat disc and moderately long tapered rays. Marginals well devel-



A



B

FIGURE 23.—*Goniaster americanus*. A, aboral; B, oral. 1 cm. indicated.

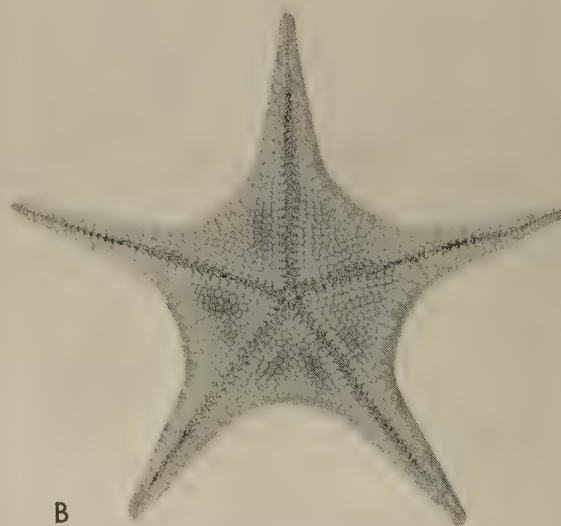
resting in depressions in plates. Adambulacral with four stout, prismatic spinules in furrow series and, on distal adambulacrals, a single large obtuse spine outside the furrow series. Rr=1.8:1. Color dark brown on top, light brown underneath.

Range:

North Carolina to Florida and the West Indies, 55 to 235 m. Taken mainly from the edge of the shelf off Cape Lookout.



A



B

FIGURE 24.—*Mediaster bairdii*. A, aboral; B, oral. 3 cm. indicated.

oped, granulated, numerous, upper and lower series nearly equal. Aboral plates longitudinally arranged, roundish, moderate in size, covered with rosette of short, obtuse spinules, sometimes with a broad sessile valvular pedicellaria. Adambulacrals with marginal row of three to seven slender spinules, sometimes with two to three bladed clavate pedicellariae. Actinal plates angular, in rows parallel to ambulacral grooves, covered with rosette of granules. $Rr=3.3:1$. Color brilliant red abactinally, salmon orange actinally.

Range:

Northeast coast of the United States, 90 to 360 m. Our only record is from the edge of the shelf off Cape Lookout.

***Plinthaster dentatus* (Perrier)**

Synonymy:

Pentagonaster dentatus Perrier, 1883.

Pyrenaster dentatus (Perrier), Verrill, 1899.

Plinthaster dentatus (Perrier), Fisher, 1911.

Description:

Form flat, more or less pentagonal, rays short. Marginals rather large, both series similar and paired. The distal inferomarginal behind the ocular plate smaller than the others; ocular plate somewhat pointed. Marginals closely covered with granules in young specimens, but with scattered clumps of granules in older specimens. Pedicellariae on adambulacrals rare, similar to granules, with short chisel-shaped blades. Adambulacral plates large, squarish; furrow spinelets in regular series, well separated from granules of actinal surface. Actinal plates polygonal, flat, crowded. Abactinal plates rounded, convex, usually with a border of granules. Papular pores not numerous confined to median radial area. $Rr=1.5:1$. Color bright orange or yellow.

Range:

North Carolina to Gulf of Mexico, 360 to 915 m. Recovered from a *Lophelia* coral reef on the slope southeast of Cape Lookout.

***Peltaster planus* Verrill**

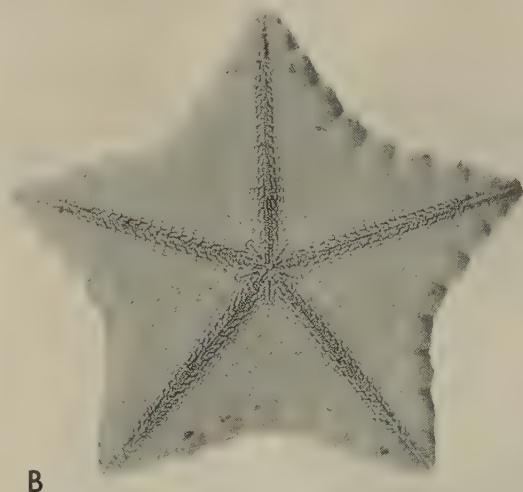
Synonymy:

Pentagonaster planus Verrill, 1885.

Peltaster planus: Verrill, 1899.



A



B

FIGURE 25.—*Plinthaster dentatus*. A, aboral; B, oral. 1 cm. indicated.

Description:

Body pentagonal, sides almost straight, rays five, triangular, obtuse. Marginals large, quadrangular, 14 in superomarginal series, 16 in inferomarginal series, covered with coarse granules (which easily rub off, sometimes leaving the superomarginals nearly bare). Aboral plates large, rounded or hexagonal, with many smaller secondary plates interspersed. All covered with rather uniform coat of granules. Actinal plates large,

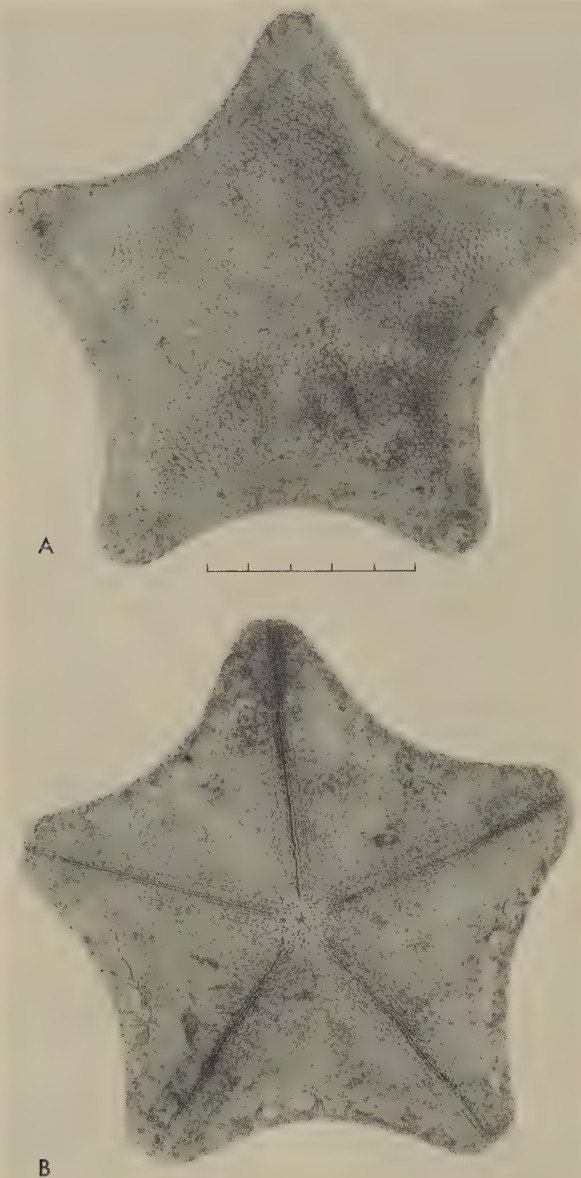


FIGURE 26.—*Pellaster planus*. A, aboral; B, oral. 5 cm. indicated.

rhombic, covered with granules. Adambulacra numerous, crowded, with 3 to 4 marginal spines in row; outside of these are 9 to 12 thicker, obtuse spines in four irregular rows; all adambulacral spines resemble the actinal granules, which are large, angular. No pedicellariae. $Rr=1.4:1$. Color pale yellowish brown.

Range:

Cape Cod to Cape Hatteras, 180 to 365 m. North Carolina specimens have come mainly from north of Cape Hatteras.

SPINULOSIDA

None of the species of the Order Spinulosida are common in North Carolina. Although the two "northern" species are very abundant north of the State, they are rarely taken in North Carolina waters. The "southern" species have been taken only in Onslow Bay.

***Solaster caribbaeus* Verrill, 1915**

Description:

Disc rather large, arms six to eight. Dorsal surface covered with numerous paxillae which are crowned with many long fine spinules. Papulae in rather regular rows from center out along arms. Inferomarginals conspicuous, forming distinct fringe around border; superomarginals not distinct from dorsals. Adambulacra with inner furrow comb of three to four webbed spines and outer transverse comb of about four larger spines. Oral spines eight, with middle two largest and longest. Anus central, protected by spines of adjacent paxillae. Madreporite inconspicuous. Species known only from small, probably juvenile specimens. $Rr=2.6:1$. Color in life unknown, preserved, pale beige.

Range:

Known previously only from the West Indies, 30 to 230 m. A single specimen has been taken from a reef in Onslow Bay.

***Porania insignis* Verrill, 1885**

Description:

Convex disc, five short rays. Dorsal surface smooth, covered with thick, leathery skin. Papulae elongate, in irregular bands from near center of disc out along either side of rays; single or double row between superomarginals and inferomarginals. Lower marginals with one to four sharp, conical, skin-covered spines, forming fringe around body. Adambulacra with transverse row of two to three short stout spines, webbed at base, outer one stoutest. Two short, skin-covered oral spines on each jaw, and two to three on each side of jaw. Actinal radial furrows conspicu-

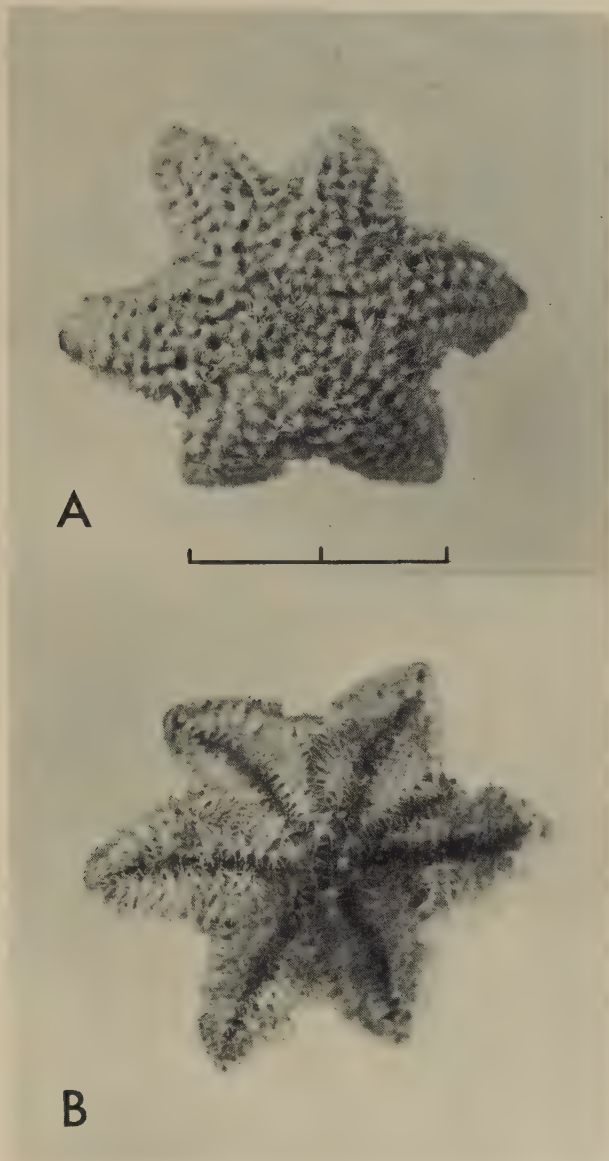


FIGURE 27.—*Solaster caribbaeus*. A, aboral; B, oral. 2 cm. indicated.

ous. $Rr=1.6:1$. Color red or reddish brown above, cream or white below.

Range:

Cape Cod to Cape Hatteras, 35 to 680 m. Seemingly limited in North Carolina to the area north of Cape Hatteras.

Thyraster serpentarius (Mueller and Troschel)

Synonymy:

Echinaster serpentarius Mueller and Troschel, 1842.



FIGURE 28.—*Porania insignis*. A, aboral; B, oral. 3 cm. indicated.

Thyraster serpentarius Ives, 1890.

Description:

Disc small, arms five, subcylindrical. Skeleton of quadrangular plates, overlapping at their corners, and arranged in very regular longitudinal series. Three to four small spines on distal edge of dorsal plates. Three to four spines on distal margin of adambulacral plates, with a small furrow spinelet. Tips of all spines thorny; plates minutely tuberculated. Papular areas rounded, regular, with



FIGURE 29.—*Thyrastra serpentarius*. A, aboral; B, oral.
3 cm. indicated.

about 10 pores per area. Madreporite raised, channeled, warty. $Rr=4:1$. Color reddish brown.

Range:

North Carolina to Florida, Alabama, and Louisiana; Vera Cruz, Mexico, 9 to 75 m. In

North Carolina mainly on reefs in Onslow Bay.

***Henricia sanguinolenta* (Sars)**

Synonymy:

- Asterias sanguinolenta* Müller, 1777.
- Asterias pertusa* Müller, 1777.
- Asterias oculata* Pennant, 1777.
- Asterias spongiosa* Fabricius, 1780.
- Asterias seposita* Retzius, 1783.
- Linckia oculata*: Forbes, 1839.
- Henricia oculata*: Gray, 1840.
- Cribella oculata*: Forbes, 1841.
- Echinaster oculatus*: Mueller and Troschel, 1842.
- Echinaster sanguinolentus* Sars, 1844.
- Echinaster sarsii* Mueller and Troschel, 1842.
- Linckia pertusa*: Stimpson, 1853.
- Cribella sanguinolenta*: Lütken, 1857.
- Cribella oculata*: Fischer, 1869.
- Henricia sanguinolenta*: Grieg, 1896.

Description:

Disc small, rays five, slender, pointed, cylindrical. Disc and arms evenly covered with small spinules on network of fine, closely reticulate plates. Papular pores numerous. Superomarginals small, indistinct, like aboral plates; inferomarginals larger. Adambulacrals transversely oblong. One to two furrow spines; actinal face of adambulacrals with numerous fine spinules. No pedicellariae. $Rr=5-7:1$. Color commonly bright red, but may be orange, green, purple, or brown.

Range:

Circumboreal and south to about lat. 35° N., 55 to 2,400 m. Rare in North Carolina and limited to the cold waters north of Cape Hatteras.

***Echinaster spinulosus* Verrill, 1869**

Description:

Disc small, rays five, long, slender, tapered. Fifteen to 20 rows of 40 or more small, conical, subacute spines on aboral plates, often 2 or 3 to a plate. The two rows of marginals larger and more rounded than abactinal plates, and with a well defined patch of glassy granules. Each also bears one small conical spine. Most of the aboral plates also have a patch of glassy granules. Papular pores numerous, but none below inferomarginals. Adambulacrals with two small furrow spines and a stouter, conical



FIGURE 30.—*Henricia sanguinolenta*. A, aboral; B, oral.
5 cm. indicated.

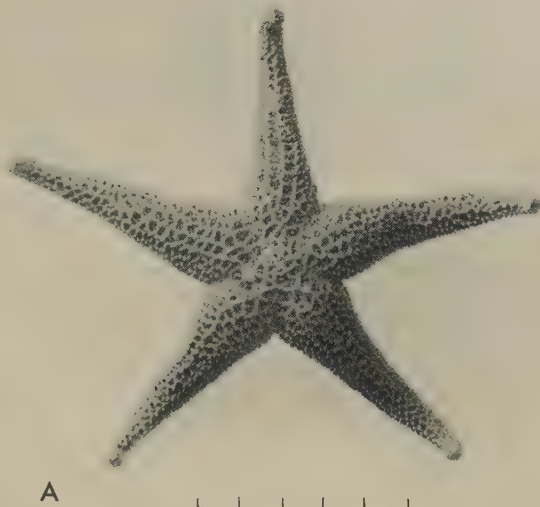


FIGURE 31.—*Echinaster spinulosus*. A, aboral; B, oral.
3 cm. indicated.

spine on the outer margin. Madreporite prominent, flattish, wartlike. The whole body invested in moderately thick dermis. $Rr=4:1$. Color dark red, purple, or reddish brown.

Range:

North Carolina to west coast of Florida and Gulf of Mexico, shore to 60 m. Found on reefs in Onslow Bay. Seemingly reported in North Carolina for the first time by Pearse and Williams (1951) from a reef off New River Inlet.

Echinaster sentus (Say)

Synonymy:

Asterias sentus Say, 1825.

Echinaster sentus: Lütken, 1871.

Description:

Disc small, rays five, of moderate length, rounded. Aboral spines in five irregular rows, median row most distinct. Larger aboral plates sometimes have two to three spines, but usually one. Two marginal rows of plates



A



B

FIGURE 32.—*Echinaster sentus*. A, aboral; B, oral. 3 cm. indicated.

fairly regular, but do not differ from other plates in size or form. Superomarginals with one stout, conical spine, on mammiform base, on each plate. A single row of small oblong plates connects the inferomarginals with the adambulacrals. Adambulacral spines small, subacute, in oblique transverse series of three. Two webbed furrow spines, inner one much smaller. Papulae numerous, papular areas large, extending to adambulacrals. Madre-

porite raised, flat, covered with rough spinules. $Rr=4:1$. Color dark red or purple.

Range:

North Carolina to West Indies, shallow water. Found on reefs in Onslow Bay, often in association with *E. spinulosus*.

Echinaster brasiliensis Mueller and Troschel

Synonymy:

(?) *Othilia brasiliensis* A. Agassiz, 1869.

Echinaster brasiliensis Mueller and Troschel, 1842.

Description:

Disc small, rays five, slender, terete. Dorsal spines small, sturdy, acute-conical, in 9 to 11 rows. Marginals not distinct from aborals. Papular areas of moderate size, numerous on aboral surface, less numerous on oral surface. Three adambulacral spines: furrow spine small, curved, two outer spines sturdy, divergent, subequal. Madreporite small, warty, covered with rough spinules. $Rr = 5:1$. Color rust red above, paler below.

Range:

North Carolina to Florida and Brazil, shallow water. Our only locality record for this species is at the edge of the shelf northeast of Cape Hatteras.

FORCIPULATIDA

All North Carolina species in the Order Forcipulatida may be found north of Cape Hatteras, and a few also occur south of the Cape. The well-known and widespread shallow water *Asterias forbesii* is the most abundant. North of Cape Hatteras, the tropical species *Coscinasterias tenuispina* and *Stephanasterias gracilis* occur only near the outer edge of the shelf.

Asterias forbesii (Desor)

Synonymy:

Asteracanthion forbesii Desor, 1848.

Asterias arenicola Stimpson, 1862.

Asterias forbesii: Verrill, 1866.

Description:

Disc moderate, often domed. Rays five, stout, cylindrical, blunt. Upper surface a firm mosaic of strong interlocking plates, each bearing a single large, blunt, rough-tipped spine encircled by a few smaller spines. Small pedicellariae encircle each spine, and larger pedicellariae are scattered over the surface. Ad-

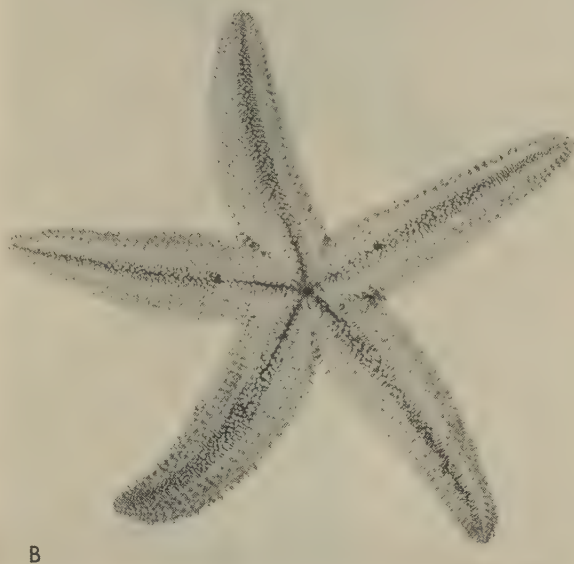
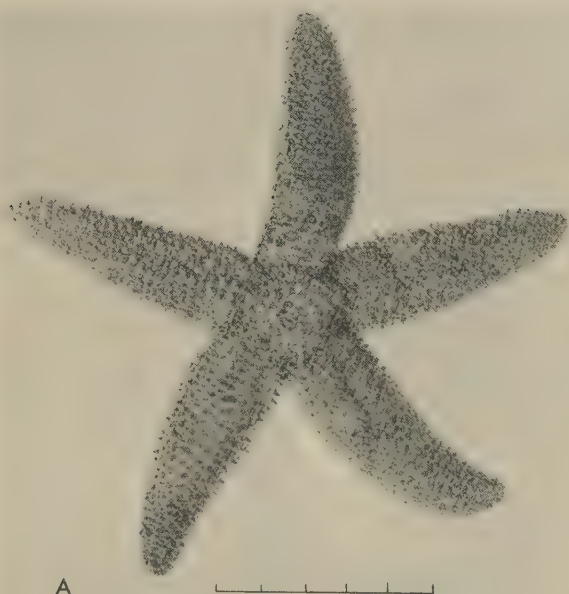
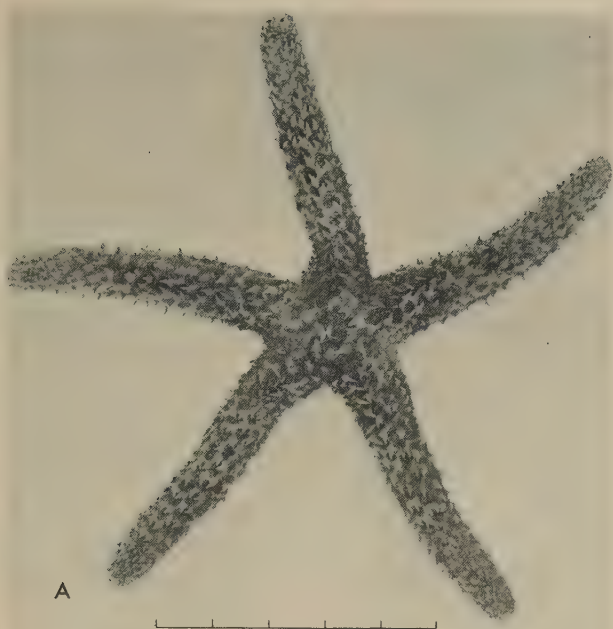


FIGURE 33.—*Echinaster brasiliensis*. A, aboral; B, oral. 5 cm. indicated.

FIGURE 34.—*Asterias forbesii*. A, aboral; B, oral. 5 cm. indicated.

ambulacra with one or two flattened, truncate, long, slender spines. Madreporite small, smooth, channeled, without warts, tubercles, or spinules. $Rr=3:1$. Color reddish brown, madreporite usually bright orange or red.

Range:

Maine to Gulf of Mexico, to 92 m. This shallow

water species is the best known sea-star along the Atlantic coast and is the one most frequently used in biology classes. Large individuals, common in winter but less so in summer, inhabit hard substrates, such as jetties, pilings, shell bottoms, and wrecks, in shallow water along the North Carolina coast and

in the estuaries. In summer, the trawls of commercial fishermen take many small individuals.

Asterias vulgaris Verrill

Synonymy:

Asterias vulgaris Packard, 1863 (nomen nudum).

Asterias stimpsoni Verrill, 1866.

Asterias vulgaris Verrill, 1866.

Asterias pallida: Perrier, 1875.

Asterias fabricii Perrier, 1875.

Description:

Disc of moderate size, arms five, more flattened and pointed than in *A. forbesii*. Aboral surface a network of narrow barlike plates with large meshes, making a fairly weak skeleton. Clearly perceptible row of median plates. All plates with one or more blunt spines with rough tips, encircled by a wreath of blunt pedicellariae. Large acute pedicellariae along sides of arms, rising directly from dermis. Inferomarginals with conspicuous series of long, truncate spines. Adambulacrals with one or two long, flattened spines. $Rr=3:1$. Color reddish brown, madreporite usually yellow.

Range:

Labrador to Cape Hatteras, shore to 650 m. Uncommon in North Carolina, where it is limited to the cold waters north of Cape Hatteras.

Asterias tanneri Verrill, 1880

Description:

Disc small, arms five, slender, terete. Aboral spines blunt, rather large and conspicuous, encircled with wreath of small pedicellariae about half way up the spine. Adambulacrals long, slender. Jaw plates long, narrow, with two pairs of large, conspicuous spines. Madreporite very small. $Rr=5.5:1$. Color pale yellowish.

Range:

New Jersey to Cape Hatteras, 35 to 350 m. In North Carolina it has been taken at several stations north of Cape Hatteras.

Coronaster briareus (Verrill)

Synonymy:

Asterias briareus Verrill, 1882.

"near *Asterias volsellata*" Nutting, 1895.

Description:

Disc small, rays 10 to 12 slender, elongate. Aboral skeleton openly reticulate, with marked median carina. Marginal plates also form ridges. Aboral and marginal spines long, slender, acute, well separated. Large rectangular papular areas, with numerous papulae in clusters. Spines bear dense wreath of small pedicellariae. Large solitary feliped pedicellariae scattered on dermis above and below. Adambulacrals with two long, slender spines.

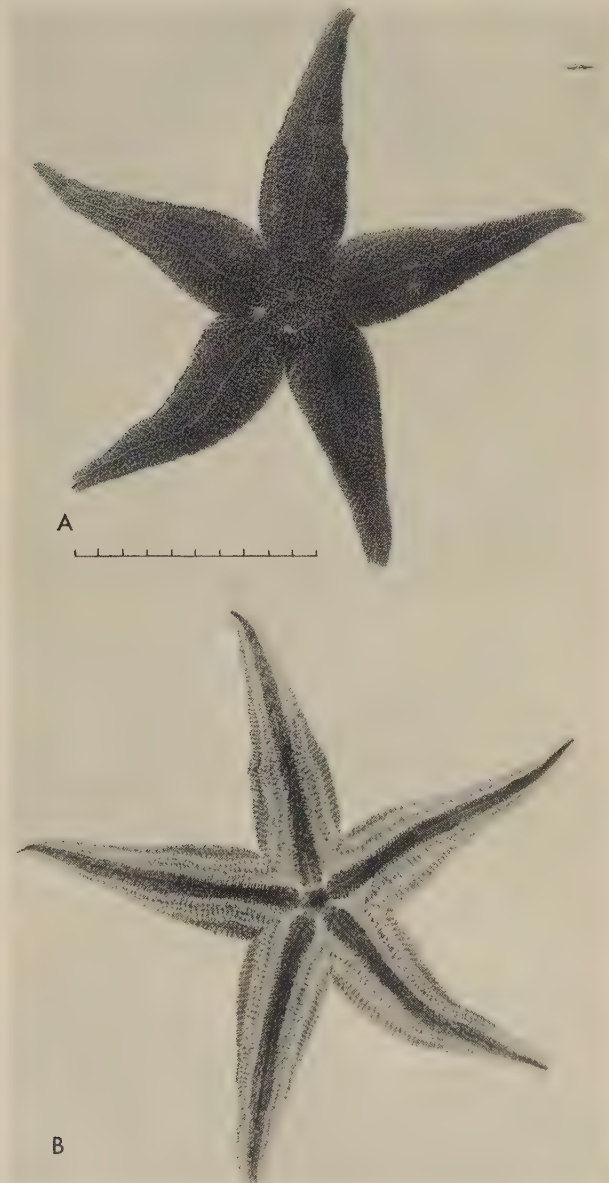
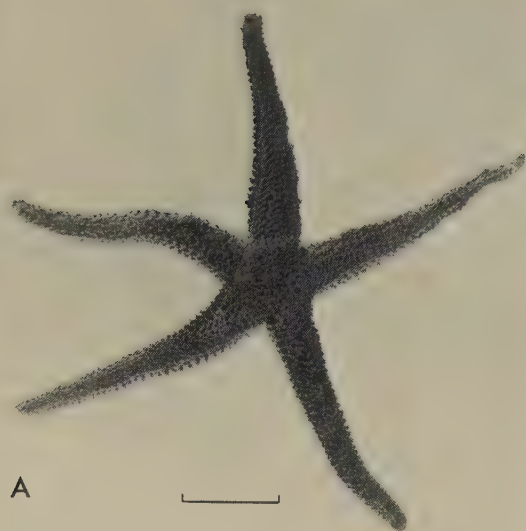


FIGURE 35.—*Asterias vulgaris*. A, aboral; B, oral. 10 cm. indicated.



A



B

FIGURE 36.—*Asterias tanneri*. A, aboral; B, oral. 1 cm. indicated.

Rr=9.5:1. Color in life unknown; preserved, pale beige.

Range:

Virginia to Key West, Fla., 35 to 75 m. So far this species has been found at only one station—North of Cape Hatteras in about 40 m.



A



B

FIGURE 37.—*Coronaster briareus*. A, aboral; B, oral. 5 cm. indicated.

Coscinasterias tenuispina (Lamarck)

Synonymy:

Asterias tenuispina Lamarck, 1816.

Asteracanthion tenuispinus: Mueller and Tro-schel, 1842.



FIGURE 38.—*Coscinasterias tenuispina*. A, aboral; B, oral. 1 cm. indicated.

Asterias (*Stolasterias*) *tenuispina*: Sladen, 1889.

Coscinasterias tenuispina: Verrill, 1914.

Asterias atlantica (pars) Verrill, 1868.

Description:

Disc small, rays four to nine (most commonly seven), long, slender, angular. Aboral and marginal spines elongate and slender. Aboral

plates form definite carinal row and one main dorso-lateral row on each side; each plate with one spine. Superomarginals and inferomarginals with one or two spines, longer than aboral spines. Adambulacrals with one long slender spine. Usually two or more madreporites present. $Rr=10:1$. Color yellowish brown, with darker markings.

Range:

Mediterranean, Madiera, Canary Islands, Cape Verde Islands, Brazil, Cuba, Bermuda, West Indies. In North Carolina, 20 to 165 m. South of Cape Hatteras it has been found on reefs off New River Inlet and Cape Lookout; north of Cape Hatteras it occurs along the edge of the shelf in 145 to 165 m.

***Stephanasterias gracilis* (Perrier)**

Synonymy:

Asterias gracilis Perrier, 1881.

Stephanasterias gracilis: Verrill, 1879.

Description:

Disc small, rays about six, often unequal, slender. Aboral surface closely covered with numerous minute slender spines, several to a plate. Marginal spines larger, flattened, and expanded at tip, which is blunt, thorny, and more or less hyaline. Adambulacrals with two short, slender, slightly clavate spines. $Rr=4.5:1$. Color in life unknown; preserved, white.

Range:

Lesser Antilles, Gulf of Mexico, Cuba, and Florida, 145 to 370 m. Although a southern species, it has been taken in North Carolina only north of Cape Hatteras—at several stations along the edge of the outer shelf.

***Leptasterias tenera* (Stimpson)**

Synonymy:

Asterias tenera Stimpson, 1862.

Asterias compta Stimpson, 1862.

Leptasterias compta: Verrill, 1866.

Description:

Disc moderate, rays five, slender, cylindrical, tapering to small blunt tip. Conspicuous slender spines rising from open network of aboral plates, no clear median row on arms. Wreath of pedicellariae around aboral spines. Adambulacrals long, blunt-tipped. Madreporite inconspicuous. $Rr = 5:1$. Color



FIGURE 39.—*Stephanasterias gracilis*. A, aboral; B, oral. 1 cm. indicated.

pale purple or pink, red eyespot at tip of arm.

Range:

Nova Scotia to North Carolina, 18 to 150 m. A cold-water species limited, in North Carolina, to the area north of Cape Hatteras in 30 to 145 m.

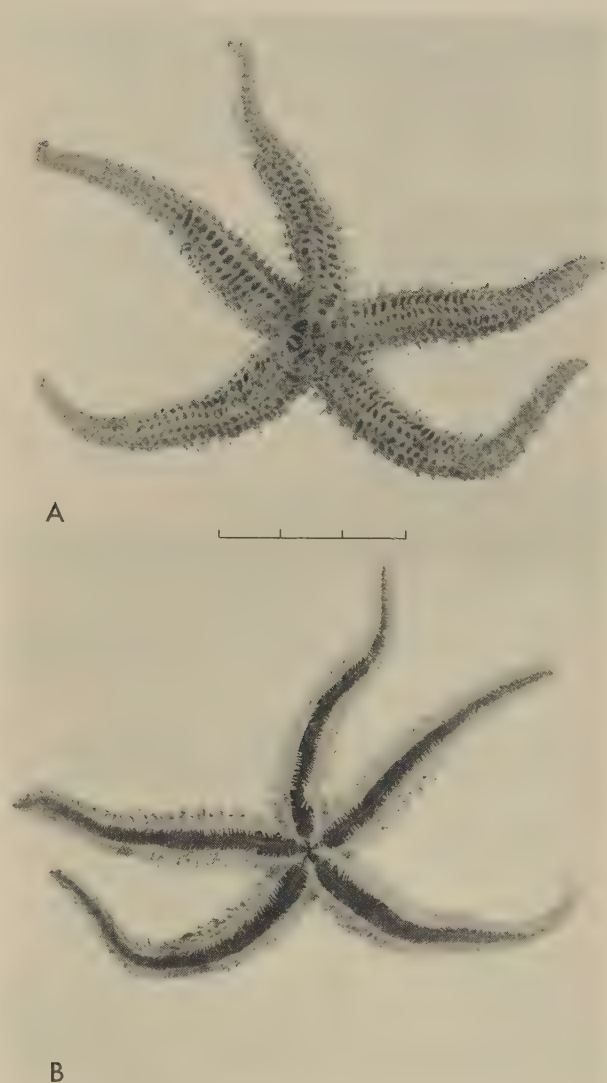


FIGURE 40.—*Leptasterias tenera*. A, aboral; B, oral. 3 cm. indicated.

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ABUNDANCE AND DISTRIBUTION OF THE LARVAE OF THE PINK SHRIMP (*PENAEUS DUORARUM*) ON THE TORTUGAS SHELF OF FLORIDA, AUGUST 1962–OCTOBER 1964^{1,2}

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ABSTRACT

A 2-year study has shown that an estimated 870×10^{10} first protozoae of pink shrimp are produced each year within the main part of the Tortugas spawning grounds. Survival rates are nearly constant and average 80.4 percent per day throughout larval life. Estimates of larval survival at specific sampling stations are influenced by the migration patterns of the larvae and vary considerably, depending on whether the sampling station receives older larvae from adjacent areas or loses larvae to other areas.

An investigation of bottom currents on the Tortugas grounds has shown that the prevailing westerly and

southwesterly currents may carry the larvae into the Florida Current, which, in turn, may transport the larvae to the nursery grounds in the Everglades National Park.

Spawning, measured by the relative abundance of first protozoae, is influenced by moon phase; most spawning occurs during the last half of the lunar month. Spawning activity reaches a maximum when bottom water temperatures are highest; the center of spawning shifts from shallow water into deeper water as the spawning season progresses.

PROCEDURES

The methods we have used covered four activities: selection of study stations, sampling procedures, laboratory techniques, and computer conversion of data.

STUDY AREA

The early life history of the pink shrimp, *Penaeus duorarum* Burkenroad, has received considerable attention in recent years. Dobkin (1961) described the early larval stages of *P. duorarum* hatched from eggs spawned in the laboratory, and Ewald (1965) succeeded in rearing all stages in the laboratory. These studies have provided evidence upon which identifications of the larvae in the plankton can be based. Eldred, Williams, Martin, and Joyce (1965) studied the inshore and offshore distribution and abundance of larval and postlarval *P. duorarum* in the Tampa Bay area. Jones, Dimitriou, Ewald, and Tweedy (unpublished manuscript)⁶ described the distribution of pink shrimp larvae over a wide area of the Tortugas Shelf of Florida and located the main spawning grounds.

The purposes of the study reported here were to (1) define quantitatively the seasonal abundance of the planktonic shrimp larvae in the main spawning area on the Tortugas Shelf; (2) investigate the relation between spawning intensity and environmental factors; (3) estimate the mortality rates of various larval stages; and (4) describe how immigration and emigration of larvae affect mortality estimates pertaining to specific sampling stations.

We sampled on a grid system that covered the Tortugas Shelf area (fig. 1); stations were 18.5 km. apart. Ten stations were selected for regular sampling in the area considered by Jones et al. (footnote 6) to be the center of spawning. The stations are designated 50.100, 50.90, 50.80, 50.70, 40.90, 40.80, 40.70, 40.60, 32.70, and 30.58 and were located over depths between 10 and 36 m. (5.5 and 20.0 fathoms). (The latter two stations

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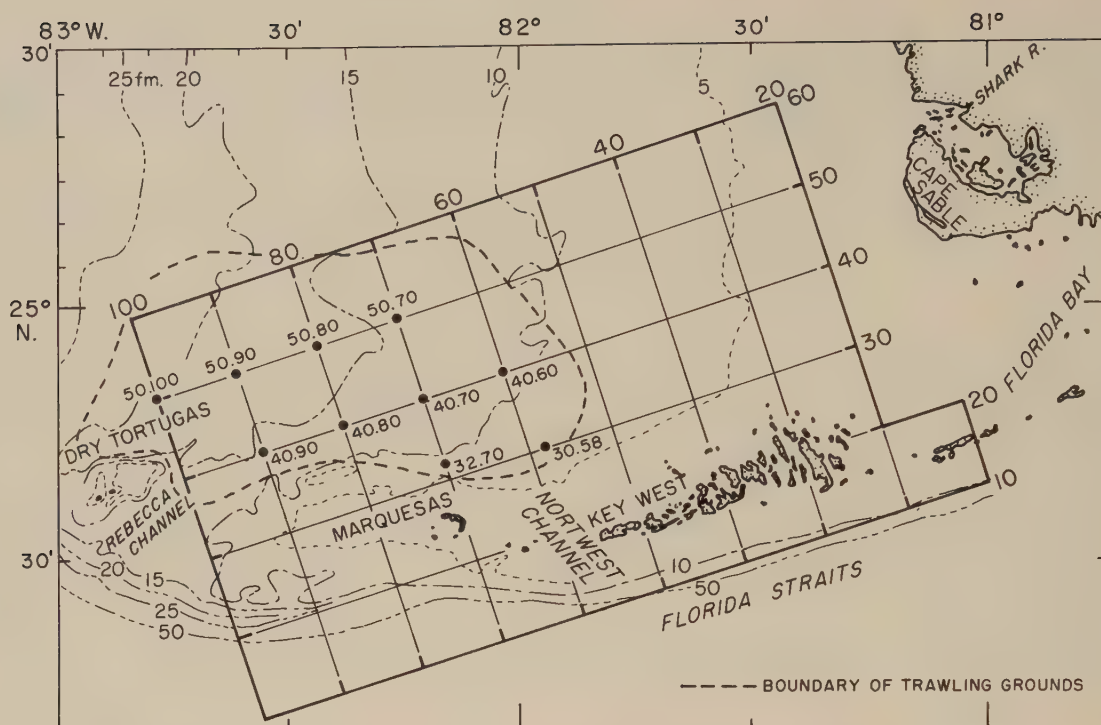


FIGURE 1.—Map of the Tortugas Shelf area showing the sampling grid, regular sampling stations, and place names mentioned in the text.

were slightly displaced from their theoretical grid coordinates because of shoal waters.)

SAMPLING

Throughout the study, we sampled about twice each month. A shrimp trawler 20 m. long overall, having an idling speed of 5.6 km. per hour (3 knots), towed the sampling apparatus. Towing speed varied according to wind velocity and at times was as low as 2.8 km. per hour (1.5 knots).

Gulf V plankton nets were used throughout the study. This net has been described by Arnold (1959) and consists of a metal frame in which is mounted a monel mesh net fitted with a brass bucket in which the plankters accumulate. The mouth diameter of the Gulf V net is 40 cm., and overall length is 100 cm. The mesh has an aperture size of 0.292 mm. Dobkin (1961) stated that first protozoae have a maximum width of 0.35 to 0.44 mm., and all subsequent larval stages are of greater size. Naupliar stages are considerably smaller (maximum width of the fifth nauplius stage is 0.17 to 0.22 mm.) and were not retained by the mesh.

Flowmeters were mounted in the mouths of the nets. These meters were calibrated regularly and

performed consistently over the entire period of operation.

Sampling procedures were rigidly controlled, and, in the event of gear failure or malfunction of timing equipment, the sample was discarded, and the tow was repeated. Replicate samples were taken at each station.

Step-oblique tows were made with the net towed for 3 minutes at each of 10 levels equally spaced between the bottom and surface. When the net was retrieved, the flowmeter reading was noted, and the bucket of plankton emptied. The net was then hosed down thoroughly, and the additional washings were added to the sample. Washing continued until no more plankton or debris appeared in the bucket. Samples were preserved with a 3-percent solution of buffered Formalin.⁷ During the cruise of October 2–6, 1964, when 41 stations were occupied, each level was sampled for 1.5 minutes and tows were reduced to 15 minutes.

Water temperatures were recorded at each station. Surface temperatures were measured with a bucket thermometer, and a trace of the vertical

⁷ Trade names referred to in this publication do not imply endorsement of commercial products.

temperature profile was obtained with a bathythermograph. Samples of the bottom waters were obtained with a Nansen bottle; the salinity of surface and bottom waters was determined on a conductivity bridge in the laboratory. Meteorological observations were recorded in World Meteorological Organization codes.

LABORATORY TECHNIQUES

Plankton sorting was carried out under wide-field, stereoscopic microscopes fitted with variable magnification.

All penaeid shrimp larvae were removed from the samples and identified to genus by using keys developed from descriptions by Pearson (1939), Gurney (1942, 1943), and Heldt (1938). Identification of different stages of *Penaeus* larvae was based on the work of Dobkin (1961). *P. duorarum* is the only member of this genus reported in the Tortugas area (Eldred, 1959); we found no larvae of other species of this genus.

Stages of other penaeid larvae also were identified. Genera encountered included *Trachypeneus*, *Sicyonia*, *Parapenaeus*, and *Penaeopsis*, as well as three unidentifiable species. Several species of *Trachypeneus* and *Sicyonia* occur in the Tortugas area (Eldred, 1959), but the specific identity of these larvae was not determined.

One-half of one of the two samples from each station was usually sorted. The second sample was retained for counting if ambiguities in the flow-meter readings or other data should be encountered. Samples were divided into equal parts by means of a two-compartment, rotating Plexiglas cylinder similar to that designed by Folsom (McEwan, Johnson, and Folsom, 1954).

COMPUTER CONVERSION OF DATA

On the basis of the methods of Ahlstrom (1954) and Sette and Ahlstrom (1948), we designed our data analysis to produce estimates of the abundance of *P. duorarum* larvae and to put the information in a form that could be reproduced easily. The plankton analyses were punched on computer data cards and processed at the Institute of Marine Sciences.

The original counts of the number of larvae in each stage were transformed in two ways. In the first, the numbers of each stage were divided by the volume of water filtered through the Gulf V sampler, giving an estimate of the number of

larvae per cubic meter of water. In the second calculation the numbers of each stage under 10 m.² surface area were estimated by multiplying 10 times the number per cubic meter by the depth of water (in meters) at the station. Unless otherwise specified, values in this report are based upon the numbers of each stage under 10 m.² surface area. All physical and biological data gathered during this investigation were published by Munro and Dimitriou (1967).

VARIABILITY OF ESTIMATES OF LARVAL ABUNDANCE

Reproducibility of plankton hauls and confidence limits to be applied to plankton estimates based upon counts of one-half of a single sample were computed. For estimating this variability, we counted the protozoae in 47 pairs of replicate samples. After reference to the records of flow-meter volume and water depth, counts were adjusted to give estimates of numbers of protozoae present under 10 m.² of surface area (table 1).

Following the methods of Winsor and Clarke (1940) and Silliman (1946), we carried out an analysis of variance to determine the variability of these estimates. Data were subjected to a logarithmic transformation, resulting in a moderately skewed normal distribution. The results of the single-classification analysis of variance are given in table 2.

The mean square between replicate estimates is $0.07319 = \sigma E^2$. The standard deviation of a single estimate (σE) is $\sqrt{0.07319}$, or 0.27054 (a logarithmic value). The 95-percent confidence limits are the antilog of the $2\sigma E$ value, viz, $2 \times 0.27054 = 0.54108$, and the antilog is 3.476. Percentage confidence limits for the estimates are $1/3.476 \times 100$ and 3.476×100 , or 28.8 and 347.6 percent.

These confidence limits are wider than those obtained by Silliman (1946) and Strasburg (1960), who found that plankton counts at the 95-percent level should be considered significantly different if they were less than half or more than double the sample compared. In the present study, the "half-or-double" rule applies only at the 70-percent level of confidence.

The confidence limits dealt with here, however, include a greater number of sources of variation and error than those of the above-mentioned authors, because the present data were computed numbers of larvae under 10 m.² surface area; thus,

TABLE 1.—Replicate tow data for analysis of variance of catches of *Penaeus duorarum* protozoae, Tortugas Shelf, Florida, August 1962 to October 1964

Tow number	Station number	Month	Year	<i>P. duorarum</i> protozoae	
				Sample 1	Sample 2
				<i>Number per 10 m.²</i>	
3091-92	40.80	9	1962	461	437
3108-09	40.70	9	1962	1,086	2,102
3110-11	40.70	9	1962	525	823
3112-13	40.70	9	1962	564	786
3116-17	40.70	9	1962	458	708
3124-25	40.80	10	1962	134	180
3209-10	40.60	3	1963	144	290
3211-12	40.70	3	1963	137	130
3213-14	40.80	3	1963	40	9
3223-34	40.80	3	1963	31	30
3306-07	50.70	5	1963	39	39
3348-49	40.70	6	1963	90	124
3381-82	40.60	7	1963	178	195
3383-84	40.70	7	1963	663	370
3385-86	40.80	7	1963	526	382
3387-88	40.90	7	1963	757	962
3389-90	51.00	7	1963	270	192
3391-92	50.90	7	1963	147	167
3395-96	50.70	7	1963	952	742
3401-02	40.60	7	1963	509	200
3405-06	40.80	7	1963	332	362
3419-20	40.70	8	1963	113	11
3421-22	40.70	8	1963	22	99
3425-26	40.70	8	1963	740	267
3427-28	40.70	8	1963	779	299
3393-94	50.80	7	1963	862	647
3432-33	40.60	8	1963	36	94
3434-35	40.70	8	1963	177	48
3446-47	50.70	8	1963	539	200
3452-53	40.60	8	1963	58	215
3466-67	50.70	8	1963	248	143
3520-21	51.00	10	1963	16	140
3638-39	51.00	4	1964	401	459
3640-41	50.90	4	1964	204	340
3642-43	50.80	4	1964	537	707
3652-53	40.70	4	1964	751	433
3694-95	40.80	5	1964	48	163
3811-12	40.80	8	1964	75	81
3813-14	40.80	8	1964	102	264
3815-16	40.80	8	1964	29	121
3817-18	40.80	8	1964	110	377
3819-20	40.80	8	1964	720	503
3823-24	40.80	8	1964	44	85
3831-32	50.80	8	1964	29	80
3835-36	40.70	8	1964	23	109
3847-48	40.80	9	1964	328	214
3821-22	40.80	8	1964	361	268

in addition to the normal sources of variation, such as patchiness of plankton, random variations in catch, and errors in the actual counting and subsampling procedures, the estimates incorporate variation in flowmeter performance and average depth over which the oblique tows were made. More important than these factors, however, is the fact that the analysis is based not upon paired hauls, but upon replicates. Replication was necessary because of the limitations of the winch used during the work. One sample was taken while the vessel traveled in a given direction and the other while the vessel moved over the station in the reverse direction. Such a sampling method must result in greater variability than would be obtained from simultaneous hauls.

Errors involved in integrating estimates over time and space have been discussed by a number of authors; the reader is referred to the works of Taft (1960), Saville (1964), and English (1964).

TABLE 2.—Summary of analysis of variance of estimates of abundance of protozoal *Penaeus duorarum* under 10 m.² surface area on the Tortugas Shelf, Florida, August 1962 to October 1964

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ¹
Between stations.....	46	20.087	0.43667	5.97
Between replicate estimates.....	47	3.440	.07319	-----
Totals.....	93	23.527	-----	-----

¹ The large value of F indicates that significantly more of the total variation is due to differences between stations than between replicates ($P < 0.01$).

On four occasions during this investigation, several sampling stations were occupied over 24-hour periods. No consistent differences were observed between night and daytime catches, and variability appeared to be within the margins expected according to the foregoing analysis. The oblique-tow method apparently sampled all layers of the water column and counteracted sampling problems caused by diurnal vertical migrations.

SEASONAL ABUNDANCE OF LARVAE

The equation developed for Pacific sardine by Sette and Ahlstrom (1948) and Ahlstrom (1954) has been applied to the counts of first protozoae of *P. duorarum* to obtain estimates of larval production in the sampling area during the period covered by this survey.

The equation is $C = \sum (C_i W_i t_i)$, in which

C = the total number of first protozoae produced in the survey area during the period t_1

$C_i = L_i/D$

L_i = estimated number of first protozoae per 10 m.² of surface area at the i th station

D = the duration of the first protozoal stage (3 days)

W_i = the area represented by station i

t_i = the time weighting given to station i (equal to one-half the time elapsing since the preceding occupancy plus one-half the time elapsing before the succeeding occupancy)

The basic data for the analysis are given in tables 3 and 4. The area represented by each sampling station is 320 km.² (see Sette and Ahlstrom, 1948, for rationale regarding the area represented by a station) and the time weighting, t_i , is usually about 14 days.

The result of the application of the equation is a minimum estimate of total larval production, because the fraction of larvae surviving the period between spawning and metamorphosis to first protozoae (about 3.5 days, according to Ewald, 1965) is unknown. Results of the analysis are given in table 5 and illustrated in figure 2.

The only complete year for which data are available is 1963. We estimated that $60,500 \times 10^8$ first protozoae were produced. It is clear from figure 2, however, that 1963 was a poor year; fewer larvae appear to have been produced than in either 1962 or 1964. If equal weighting is allowed for all data, annual production is in the order of $87,000 \times 10^8$ first protozoae.

SEASONAL VARIATIONS IN SPAWNING INTENSITY

The percentage of the annual catch of protozoae taken in each month from 1959 to 1964 is shown in figure 3. The data are for samples taken between 18.4 and 36.7 m. (10 and 20 fathoms). Data for

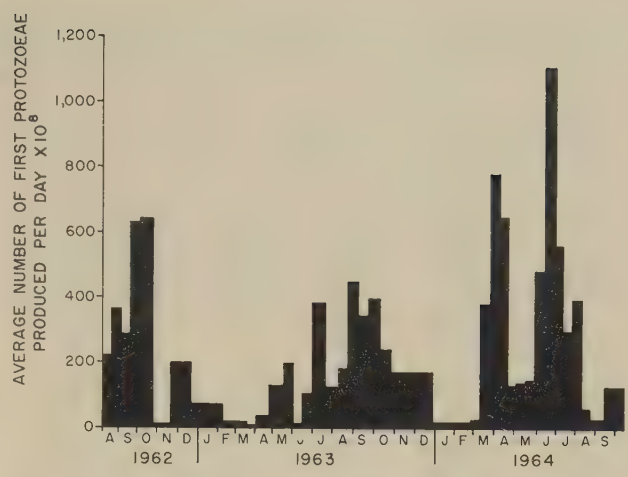


FIGURE 2.—Seasonal fluctuations in production of first protozoae of *P. duorarum* in the Tortugas Shelf area, August 1962 to October 1964.

1959 through mid-1962 are taken from Jones et al. (footnote 6) and are for catches made with the Discovery net; the more recent data are derived from the use of the Gulf V sampler. Because of

TABLE 3.—Summary of Tortugas tows: Cruise totals and physical data. All values are the sum of the computed numbers of *P. duorarum* larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964

Cruise	Date	Subtotal by stage				Total	Percentage by stages				Average number of larvae/tow	Moon age	Average bottom temperature
		Protozoae	Myses	Postlarvae			Protozoae	Myses	Postlarvae				
				1-3 spines	4+ spines				1-3 spines	4+ spines			
	1962	Number	Number	Number	Number	Number	Percent	Percent	Percent	Percent	Number	Days	° C.
6201	8/14-16	3,146.1	136.8	129.4	0	3,412.3	92.2	4.1	3.7	0	379.1	16	-----
6202	8/28-30	5,342.3	151.2	106.6	5.3	5,605.4	95.3	2.7	1.9	.1	560.5	29	26.8
6203	9/11-12	6,408.5	612.3	308.8	5.8	7,335.4	87.4	8.3	4.2	.1	733.5	13	26.2
6204	9/25-28	7,448.2	510.7	124.8	3.0	8,086.7	92.1	6.3	1.5	.1	808.7	28	28.7
6205	10/9-10	8,363.4	434.7	227.9	2.6	9,028.6	92.6	4.8	2.5	.1	902.9	12	28.7
6206	11/7-8	103.6	3.9	19.5	16.1	143.1	72.4	2.7	13.6	11.3	17.8	11	24.6
6207	12/4-5	1,923.8	52.0	0	0	1,975.8	97.4	2.6	.3	0	197.6	8	22.8
	1963												
6301	1/9-10	834.2	36.0	28.4	1.7	900.3	92.7	4.0	3.2	.2	90.0	14	20.2
6303	3/11-12	339.8	3.9	0	0	343.7	98.9	1.1	0	0	34.4	16	20.7
6304	3/26-27	126.6	11.3	6.3	0	144.2	87.8	7.8	4.4	0	14.4	2	21.1
6305	4/8-10	472.3	0	2.5	0	474.8	99.6	0	.4	0	47.5	16	20.9
6306	5/7-9	1,692.4	104.9	24.9	0	1,822.2	92.8	5.8	1.4	0	182.2	16	23.2
6307	5/20-23	2,638.6	93.0	60.4	0	2,792.0	94.5	3.3	2.2	0	279.2	29	23.1
6308	6/4-5	198.7	73.3	91.5	7.7	371.2	53.6	19.7	24.6	.1	41.2	13	22.6
6309	6/18-22	1,905.1	391.3	115.2	0	2,411.6	79.0	16.2	4.8	0	241.2	28	23.8
6310	7/1-2	5,281.2	304.1	23.6	0	5,608.9	94.2	5.4	4.2	0	560.9	11	24.7
6311	7/30-8/1	2,823.2	935.8	1,188.4	28.0	4,975.4	56.7	18.8	23.9	.6	497.5	12	29.6
6313	8/13-14	2,868.4	221.5	411.7	0	3,501.6	81.9	6.3	11.8	0	350.2	25	29.9
6314	8/27-28	9,825.5	1,219.1	341.8	0	11,386.5	86.3	10.7	3.0	0	1,138.7	9	30.1
6315	9/10-11	5,929.8	927.7	314.3	0	7,171.8	82.7	12.9	4.4	0	717.2	23	30.2
6316	10/1-2	1,380.9	1,793.6	612.7	0	9,787.2	75.4	18.3	6.3	0	978.7	15	28.9
6317	10/15-16	2,604.9	51.7	16.9	14.7	2,688.2	96.9	1.9	.6	.6	268.8	29	29.0
6318	11/5-6	3,460.1	85.3	56.8	0	3,602.2	96.0	2.4	1.6	0	360.2	20	24.9
	1964												
6401	2/17-18	131.2	39.6	0	0	170.8	76.8	23.2	0	0	21.4	5	19.1
6402	3/3-4	349.8	0	0	0	349.8	100.0	0	0	0	35.0	20	19.5
6403	3/17-18	6,389.1	277.1	6.4	0	6,672.6	95.8	4.2	.1	0	667.3	4	20.5
6404	4/1-2	16,280.3	4,198.0	1,106.5	4.5	21,589.3	75.5	19.5	5.1	.1	2,158.9	19	22.1
6405	4/14-15	8,483.8	272.0	178.9	2.0	8,936.7	95.0	3.1	2.0	.1	893.7	3	23.4
6406	4/28-30	1,599.8	147.6	196.3	0	1,943.7	82.2	7.6	10.2	0	194.4	17	24.7
6407	5/12-14	1,721.2	137.9	79.9	8.5	1,947.5	88.4	7.1	4.1	.4	194.8	2	26.2
6408	5/26-28	2,242.8	324.8	149.0	0	2,716.6	82.6	12.0	5.5	0	273.6	16	26.9
6409	6/9-11	7,225.6	409.6	89.9	0	7,725.1	93.5	5.3	1.2	0	772.5	1	27.6
6410	6/23-25	21,404.9	1,582.7	762.6	16.3	23,766.5	90.2	6.7	3.2	.1	2,376.7	14	27.1
6411	7/7-9	9,739.7	444.0	360.9	0	10,544.6	92.4	4.2	3.4	0	1,054.5	28	28.3
6412	7/21-23	4,846.2	711.4	518.6	6.6	6,082.8	79.6	11.7	8.5	.1	608.3	13	28.3
6413	8/4-5	5,887.0	406.5	304.2	4.8	6,602.7	89.2	6.2	4.6	.1	660.3	24	28.6
6414	8/18-21	1,207.9	146.8	38.6	0	1,393.3	86.7	10.5	2.8	0	139.3	12	25.5
6415	9/1-2	343.0	7.6	50.3	0	400.9	85.5	1.9	12.5	0	40.0	22	22.9
6416	10/2-6	1,725.8	38.9	9.3	0	1,774.0	97.3	2.2	.5	0	177.4	28	25.0

TABLE 4.—Summary of Tortugas tows: Cruise totals by stage. All values are the sum of the computed numbers of each larval stage of *P. duorarum* under 10 m.² surface area at 10 stations on the Tortugas Shelf,¹ August 1962 to October 1964

Year and cruise number	Stage										
	Protozoaeae			Myses			Postlarvae				
	1	2	3	1	2	3	1	2	3	4	5
1962	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number
6201	1,669.7	995.6	480.8	43.4	34.6	58.8	46.8	57.1	25.5	0	0
6202	3,201.8	1,384.3	756.2	75.5	19.0	56.7	48.1	36.3	22.2	5.3	0
6203	2,465.1	2,473.6	1,469.8	281.3	166.9	164.1	214.5	59.0	35.3	5.8	0
6204	5,508.0	1,575.7	364.5	288.4	83.4	138.9	50.4	41.5	32.9	3.0	0
6205	5,560.3	1,922.4	880.7	300.4	66.3	68.0	93.3	92.4	42.2	2.6	0
6206	64.0	39.6	0	0	0	3.9	16.2	0	7.0	16.1	0
6207	1,741.9	154.7	27.2	33.1	18.9	0	0	0	0	0	0
1963											
6301	628.3	132.3	73.6	15.6	12.6	7.8	20.2	4.1	4.1	1.7	0
6303	171.2	101.7	66.9	3.9	0	0	0	0	0	0	0
6304	63.7	37.2	25.7	11.3	0	0	2.1	2.1	2.1	0	0
6305	322.4	136.3	13.6	0	0	0	0	0	2.5	0	0
6306	1,119.1	418.0	155.3	41.7	0	63.2	24.9	0	0	0	0
6307	1,757.5	635.5	245.6	50.7	12.7	29.6	26.5	21.0	12.9	0	0
6308	93.3	46.0	59.4	23.5	6.6	43.2	21.2	52.3	18.0	5.1	2.6
6309	902.3	660.7	342.1	188.9	20.5	181.9	103.7	11.5	0	0	0
6310	3,346.6	1,501.9	432.7	210.4	46.4	47.3	11.8	6.8	5.0	0	0
6311	1,105.2	1,202.0	516.0	254.3	211.9	469.6	879.7	218.4	90.3	28.0	0
6313	1,633.3	614.4	620.7	138.8	24.1	58.6	44.5	267.3	99.9	0	0
6314	3,943.0	3,154.1	2,728.4	602.8	309.2	307.2	126.3	206.5	9.0	0	0
6315	2,976.5	1,682.8	1,270.5	631.6	120.8	175.3	208.1	82.6	23.6	0	0
6316	3,463.5	2,442.2	1,475.2	716.0	372.4	705.2	399.6	185.7	27.4	0	0
6317	2,126.2	244.0	234.7	40.4	11.3	0	5.7	5.6	5.6	14.7	0
6318	1,737.2	1,444.2	278.7	65.0	6.4	13.9	28.0	28.8	0	0	0
1964											
6401	126.9	4.3	0	12.8	6.6	20.2	0	0	0	0	0
6402	202.9	88.0	58.9	0	0	0	0	0	0	0	0
6403	3,348.6	2,190.4	850.1	185.2	53.4	38.5	6.4	0	0	0	0
6404	6,831.7	5,368.3	4,080.3	2,051.1	921.9	1,225.0	663.2	400.2	43.1	4.5	0
6405	5,662.2	2,146.4	675.2	90.4	66.3	115.3	55.3	96.7	26.9	2.0	0
6406	1,087.9	406.0	105.9	37.3	20.7	89.6	80.1	116.2	0	0	0
6407	1,219.6	361.0	140.6	69.8	38.3	29.8	11.3	32.6	36.0	8.5	0
6408	1,291.2	734.9	216.7	180.3	20.4	124.1	97.5	44.7	6.8	0	0
6409	4,210.7	1,882.9	1,132.0	228.4	103.1	78.1	38.7	51.2	0	0	0
6410	9,665.8	8,077.4	3,661.7	749.0	333.3	500.4	478.0	233.2	51.4	16.3	0
6411	4,885.3	3,195.6	1,658.8	232.2	105.4	106.4	222.1	95.4	43.4	0	0
6412	2,550.6	1,422.2	873.4	322.1	121.8	267.5	244.2	225.5	48.9	6.6	0
6413	3,447.4	1,801.0	638.6	138.8	126.2	141.5	197.0	75.4	31.8	4.8	0
6414	498.9	479.9	229.1	58.2	64.5	24.1	33.6	5.0	0	0	0
6415	206.4	72.7	63.9	3.8	3.8	0	0	50.3	0	0	0
6416	1,109.2	371.0	245.7	14.7	24.2	0	9.3	0	0	0	0

¹ The totals for cruises 6201, 6206, 6308, and 6401 are the sums of 9, 8, 9, and 8 stations, respectively.

the different sampling characteristics of the two nets, data for the first and second halves of 1962 cannot strictly be compared. The average catch of the Gulf V net per unit volume of water strained during the spawning seasons of 1963 and 1964 was about 10 times greater than the catch of the Discovery net during the spawning seasons of 1959-61. In the construction of the histograms for 1962, the numbers per 1,000 m.³ filtered by the Discovery net have been equated with the numbers per 100 m.³ filtered by the Gulf V net.

Spawning occurred throughout the annual temperature range of 19° C. to 30° C., but most spawning occurred when temperatures exceeded 25° C. and peaks were usually associated with the highest temperatures reached in each year. Highest temperatures were recorded as early as June and as late as the end of September, resulting in corresponding shifts from year to year in the main time of spawning.

SEASONAL RELATION BETWEEN DEPTH AND SPAWNING

In general, a seasonal shift was observed in the depth at which most spawning (as measured by the presence of first protozoa) occurred. The center of abundance of first protozoa was usually at the shallowest stations in early spring and then moved toward deeper water as the season progressed until in the fall it was at depths greater than 30 m. (16.7 fathoms). In 1962 the center of abundance of first protozoa moved from about 25 m. (13.8 fathoms) in August and September to about 32 m. (17.7 fathoms) by early November (fig. 4). In 1963 a steady movement of the center of spawning was again apparent from the shallow waters (20 to 25 m. or 11.1 to 13.8 fathoms) in early spring to a depth of 36 m. (20 fathoms) in early November. This movement was not as apparent in 1964, possibly because maximum spawning occurred earlier in the year.

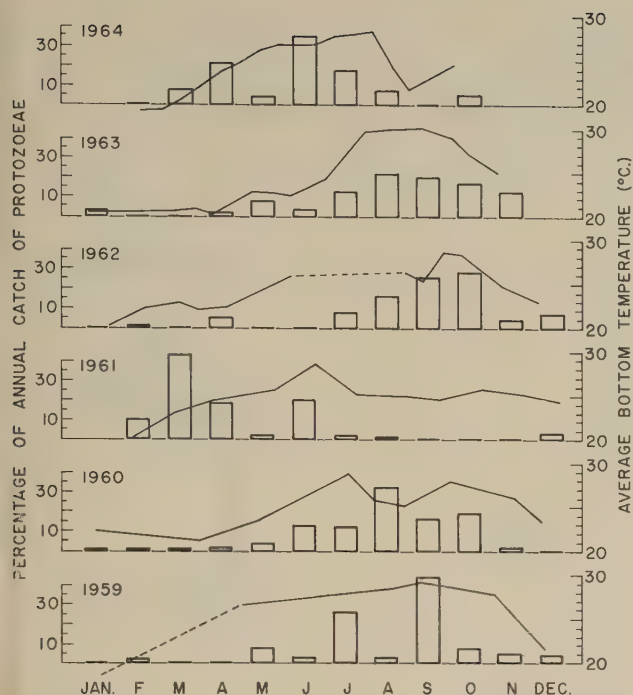


FIGURE 3.—Histograms showing the relation between the percentage of the annual catch of first protozoae taken in each month, and (solid lines) the average bottom water temperature from the Tortugas Shelf area, 1959–64. Broken lines indicate no data.

An analysis of the distribution of bottom temperatures suggests that temperature plays no significant part in the movement of the center of spawning. During 1963, when the movement into deeper water was most marked, bottom temperatures appeared to be almost uniform at any given time throughout the sampling area. Shrimp landing data for 1963 (U.S. Fish and Wildlife Service, 1964) showed that small shrimp appeared in the shallow areas of the trawling grounds about April and again in October. Previous studies of adult shrimp (Iversen and Jones, 1961; Iversen, Jones, and Idyll, 1960; and Iversen and Idyll, 1959) have shown that the average size of shrimp increases with increasing depth. Shrimp tagging studies also have indicated a migration toward deeper water. Apparently the maturing shrimp entering the fishery in the early part of the summer begin spawning when they reach a suitable size and continue to spawn as they migrate to deeper water. This theory is compatible with data on maturation and growth provided by Eldred, Ingle, Woodburn, Hutton, and Jones (1961) and by Iversen (1962).

TABLE 5.—Estimates of the production of first protozoae of *P. duorarum* on the Tortugas Shelf, August 1962 to October 1964

Cruise	Date	Length of inter-cruise period	First proto-zoae produced during inter-cruise period	Average number of first protozoae produced per day
<i>1962</i>				
	<i>Days</i>		<i>Calculated number × 10⁸</i>	
6201	Aug. 14–16	14.0	2,993.0	213.8
6202	Aug. 28–30	13.8	5,091.9	369.0
6203	Sept. 11–12	14.3	4,062.2	284.1
6204	Sept. 25–28	14.0	8,886.2	634.7
6205	Oct. 9–10	21.0	13,455.5	640.7
6206	Nov. 7–8	28.0	258.5	9.2
6207	Dec. 4–5	32.0	6,423.0	200.7
<i>1963</i>				
6301	Jan. 9–10	48.5	3,511.0	72.4
6303	Mar. 11–12	38.0	750.1	19.7
6304	Mar. 26–27	14.3	104.8	7.3
6305	Apr. 8–10	21.3	791.6	37.2
6306	May 7–9	21.3	2,746.6	129.0
6307	May 20–23	13.8	2,794.7	202.5
6308	June 4–5	14.8	177.0	12.0
6309	June 18–22	13.5	1,403.9	104.0
6310	July 1–2	20.8	8,021.3	385.6
6311	July 30–Aug. 1	21.5	2,738.2	127.4
6313	Aug. 13–14	13.5	2,540.8	188.2
6314	Aug. 27–28	13.5	6,134.0	454.4
6315	Sept. 9–10	17.5	6,002.7	343.0
6316	Oct. 1–2	18.0	7,184.2	399.1
6317	Oct. 15–16	17.5	4,287.6	245.0
6318	Nov. 5–6	64.5	11,352.1	176.0
<i>1964</i>				
6401	Feb. 17–18	59.0	1,079.0	18.3
6402	Mar. 3–4	14.0	327.2	23.4
6403	Mar. 17–18	14.5	5,595.3	385.9
6404	Apr. 1–2	14.0	11,021.5	787.3
6405	Apr. 14–15	13.8	9,004.4	652.5
6406	Apr. 28–30	14.3	1,792.6	125.4
6407	May 12–14	14.0	1,967.4	140.5
6408	May 26–28	14.0	2,083.1	148.8
6409	June 9–11	14.0	6,793.4	485.2
6410	June 23–25	14.0	15,593.8	1,113.8
6411	July 7–9	14.0	7,881.4	563.0
6412	July 21–23	13.8	4,056.2	293.9
6413	Aug. 4–5	14.3	5,680.8	397.3
6414	Aug. 18–21	14.0	864.9	57.5
6415	Sept. 1–2	22.3	530.4	23.8
6416	Oct. 2–4	30.0	3,834.3	127.8

INTRAMONTHLY VARIATIONS IN SPAWNING—THE EFFECT OF MOON PHASE

The percentage of various larval stages in the total catch varied considerably on successive cruises. We analyzed these variations to determine whether they could in some way be related to the lunar phases.

The percentage which first protozoae represented in the total catch of larvae and postlarvae taken on each cruise was calculated and plotted against moon age minus 5 days (table 6). The average age of first protozoae is 5 days (Ewald, 1965), and subtracting 5 days backdates the observation of the relative abundance of protozoae to the time of spawning. The average of the percentages of protozoae in all catches was 50.6 percent; in 12 of 18 catches taken during the waxing moon (0–14.7 days) the relative abundance of first protozoae was below average (fig. 5), whereas in 11 of 17 catches during the waning moon the relative abundance was above average.

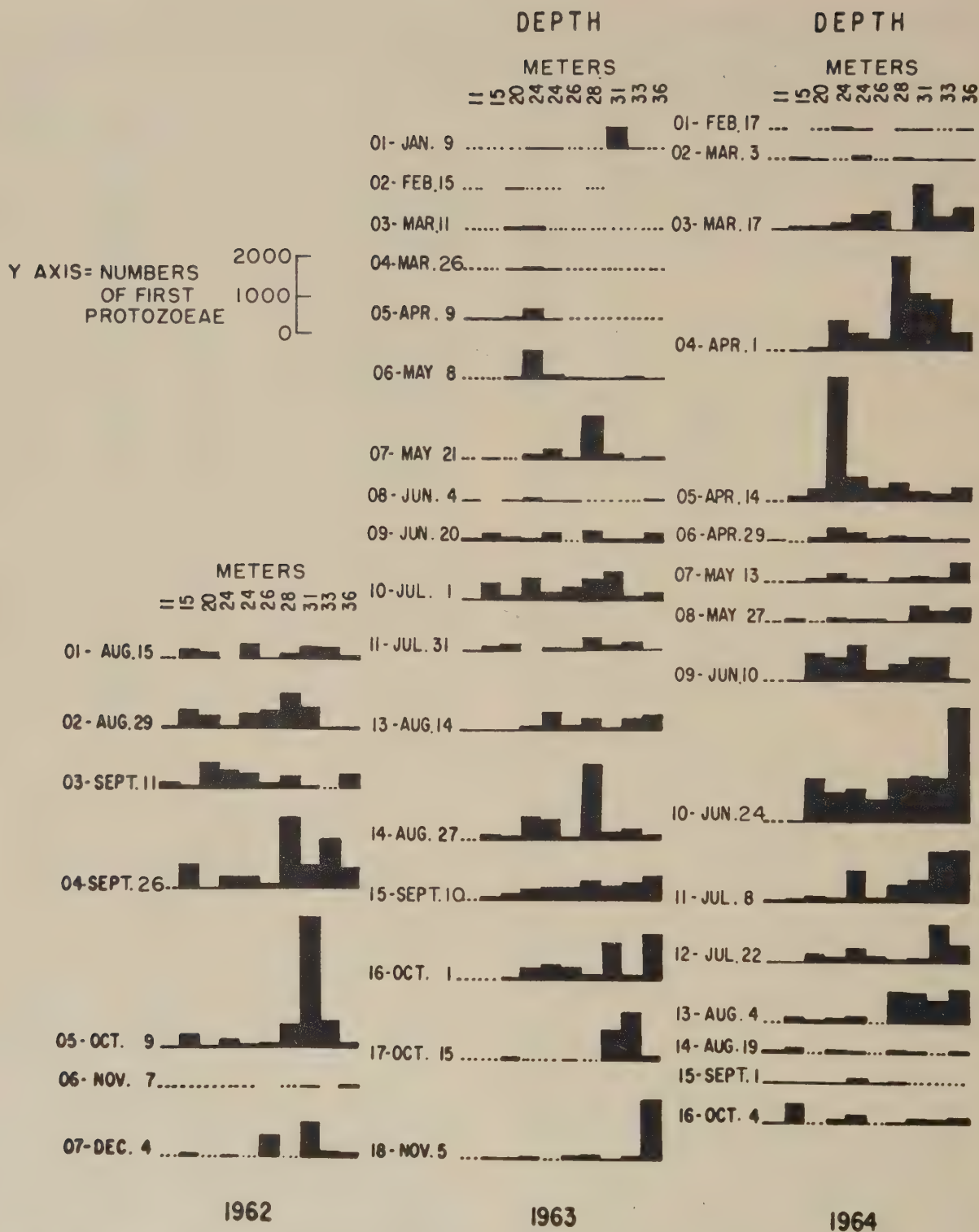


FIGURE 4.—Histograms showing the seasonal movement of the center of abundance of first protozoae of *P. duorarum* from shallow-water stations toward deepwater stations, Tortugas Shelf, Fla., August 1962 to October 1964. Numbers preceding dates indicate cruise numbers.

PERCENTAGE OF 1ST PROTOZOEAE
IN TOTAL

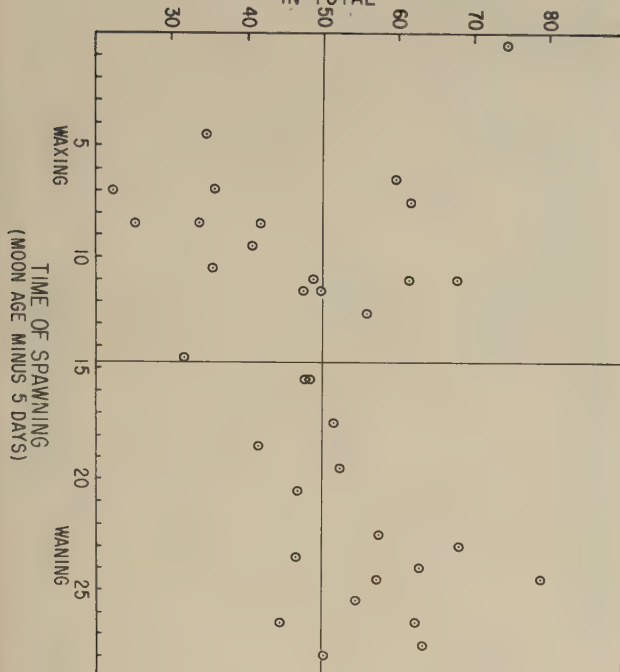


FIGURE 5.—The relation between moon phase and relative spawning intensity (as measured by the relative abundance of first protozoeae) in the Tortugas Shelf area, August 1962 to October 1964.

Using a chi-square test, we found that the probability of such a distribution arising by chance is slight (<0.02); we conclude, therefore, that spawning occurs mainly during the last half of the lunar month. That most spawning occurs in the last half of the lunar month agrees with the observations of Korrunga (1957), who stated that in animals showing lunar periodicity in spawning, the spawning is often concentrated around the last lunar quarter. He suggested that this concentration is a result of a photoperiodic effect, the final stages of maturation of the gonads being triggered by the greater exposure to light during the full-moon period. This photoperiodic effect on maturation may also hold for *Penaeus*, but the advantages of lunar periodicity are obscure because copulation occurs in advance of spawning (Hudinaga, 1942, for *P. japonicus*), and all eggs are fertilized at extrusion. Alternating periods of high and low larval density may be advantageous in that they prevent a concentrating of major predators, thus reducing mortality caused by prolonged predation.

TABLE 6.—Data for the analysis of the effect of moon phase on rate of spawning of *P. duorarum*; all data are in terms of estimated numbers of larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964

Year and cruise number	Date	First protozoeae	Total larvae	Percentage of first protozoeae in total catch	Time of spawning (moon age minus 5 days)
1962		Number	Number	Percent	Days
6201	Aug. 14-16	1,669.7	3,412.3	48.9	10-12
6202	Aug. 28-30	3,201.8	4,605.4	57.1	24-25
6203	Sept. 11-12	2,465.1	7,335.4	33.6	8-9
6204	Sept. 25-28	5,508.0	8,086.7	68.1	22-24
6205	Oct. 9-10	5,560.3	9,028.6	61.6	7-8
1963					
6303	Mar. 11-12	171.2	343.7	49.8	11-12
6304	Mar. 26-27	63.7	144.2	44.2	26-27
6305	Apr. 8-10	322.4	474.8	67.9	10-12
6306	May 5-7	1,119.1	1,822.2	61.4	10-12
6307	May 20-23	1,757.5	2,792.0	62.9	23-25
6308	June 4-5	93.3	371.2	25.1	8-9
6309	June 18-22	1,145.1	2,411.6	57.5	22-23
6310	July 1-2	3,346.6	5,608.9	59.7	6-7
6311	July 30-Aug. 1	1,105.2	4,975.4	22.2	6-8
6313	Aug. 13-14	1,633.3	3,501.6	46.6	20-21
6314	Aug. 27-28	3,943.0	11,386.5	34.6	4-5
6315	Sept. 10-11	2,976.5	7,171.8	41.5	18-19
6316	Oct. 1-2	3,463.5	9,787.2	35.4	10-11
6317	Oct. 15-16	2,126.2	2,688.2	79.1	24-25
6318	Nov. 5-6	1,737.2	3,602.2	48.2	15-16
1964					
6401	Feb. 17-18	126.9	170.8	74.2	0-1
6402	Mar. 3-4	202.9	349.8	58.0	15-16
6403	Mar. 17-18	3,348.6	6,672.6	50.2	27-29
6404	Apr. 1-2	6,831.7	21,589.3	31.6	14-15
6405	Apr. 14-15	5,662.2	8,936.7	63.3	27-28
6406	Apr. 28-30	1,087.9	1,943.7	55.9	12-13
6407	May 12-14	1,219.6	1,947.5	62.2	26-27
6408	May 26-28	1,291.2	2,716.6	47.5	11-12
6409	June 9-11	4,210.7	7,725.1	54.5	25-26
6410	June 23-25	9,665.8	23,766.5	40.7	9-10
6411	July 7-9	4,885.2	10,544.6	46.3	23-24
6412	July 21-23	2,550.6	6,082.8	41.9	8-9
6413	Aug. 4-5	3,447.4	6,602.7	52.2	19-20
6414	Aug. 18-21	498.9	1,393.3	35.8	5-9
6415	Sept. 1-2	206.4	400.9	51.5	17-18

MORTALITY AND MIGRATION

The two factors of larval mortality and migration toward the inshore nursery grounds are inseparable and will be dealt with concurrently. Sampling stations which lie on the migration route will always receive immigrant larvae, and, as a result, survival rates calculated from the catch of larvae at such stations will be higher than the true value; conversely, calculations of survival based upon the catch taken at stations from which larvae consistently emigrate will underestimate the true survival rates.

Totals are given in table 7 of the estimates of numbers of each larval stage under 10 m.² surface area for 37 cruises in the sampling area from August 1962 to July 1964. These estimates provide a measure of the relative abundance of each larval stage for 2 calendar years.

Calculation of survival rates on a temporal basis requires knowledge of the duration of the various larval stages. The following figures for the

average time spent in each larval stage have been derived from the information given by Ewald (1965) on the rate of development of larvae at 26° C.:

Stage	Days
Egg.....	1.5
Nauplius.....	2.0
1st protozoaea.....	3.0
2d protozoaea.....	2.4
3d protozoaea.....	2.2
1st mysis.....	2.0
2d mysis.....	2.3
3d mysis.....	3.0
1-spine postlarva.....	2.0
2-spine postlarva.....	2.0
3-spine postlarva.....	3.0
4-spine postlarva.....	3.0
5-spine postlarva.....	6.0

Growth and development of larvae in the laboratory may differ considerably from that in the ocean; however, the relative duration of the instars may be expected to be nearly constant, and in the absence of better data the times given above have been used to plot catch curves for the larvae.

Catch curves, obtained by plotting the logarithm of the total "catch" of each stage against the estimated average age of the larval stage, are shown in figure 6. A feature common to all of the curves is that the catch of first and second mysids appears to have been depressed. At all stations, the catch of second mysids was less than the catch of third mysids. Several possible explanations for this depression of the catch curve present themselves.

First, it is possible that the larvae are most active in the first and second mysis stages, and that the depressed catch of these stages reflects active avoidance of the Gulf V net. Heldt (1938)

TABLE 7.—Totals of the estimates of numbers of each larval stage of *P. duorarum* under 10 m.² surface area for 37 cruises in the Tortugas Shelf area, August 1962 to July 1964

Station	Depth	Protozoaeae			Myses			Postlarvae		
		1	2	3	1	2	3	1	2	3
	<i>M.</i>	<i>Number</i>								
50.100	36.5	12,618	5,420	2,307	591	241	452	355	43	17
50.90	33.0	11,350	5,704	3,221	1,037	263	536	209	150	0
50.80	31.0	16,040	7,497	3,151	1,039	389	520	355	146	6
40.90	27.5	14,008	6,438	2,910	1,054	272	451	182	195	17
50.70	25.5	5,020	2,841	2,145	972	434	477	436	364	180
40.80	24.0	8,572	6,841	5,087	1,194	604	955	546	541	37
40.70	24.0	10,579	7,282	4,108	949	442	786	564	428	123
40.60	20.0	5,112	4,824	1,848	1,440	506	786	1,263	367	117
32.70	14.5	3,324	1,474	783	345	127	150	159	193	102
30.58	11.0	279	472	438	215	60	152	204	244	241

NOTE. The five highest values in each column are in *italics*.

has stated that the mysids appear to be the most active larval stages.

Secondly, third mysids and older postlarvae spawned in another area (possibly to the north of the Tortugas) may drift into the Tortugas area, thus increasing the catch of the stages older than second mysis. Jones et al. (footnote 6), however, reported no evidence of any other center of spawning.

Finally, an error in the estimated time required for the shrimp to develop through the mysis stages may account for this discrepancy. Since mysis stages are rather ill-defined, allocation to first, second, or third mysis may be somewhat arbitrary, depending upon the degree of development of the pleopods and telson. More than three stages may exist at temperatures lower than 26° C. (Ewald, 1965). If average duration of mysis stages is less than the postulated 7.3 days, then the daily survival rate must decrease considerably after the third protozoal stage and then increase again during the postlarval stages.

The first alternative—avoidance of the net—suggested above is considered to be most likely. An inspection of the catch curves shows that the slope of the curves during the protozoal stages and during the stages subsequent to third mysis is fairly uniform; in a number of catch curves, the points describing the abundance of the third protozoal stage and of the third mysis stage can be joined to produce an almost uniform slope throughout the catch curve (fig. 6). This view is also supported by the work of Jones et al. (footnote 6), who found that the numbers of larvae decline steadily between the third protozoal stage and the third mysis stage. Jones et al. (footnote 6) used a Discovery net of 76-cm. mouth diameter and with larger mesh sizes than those of the Gulf V sampler. Such a net may capture a more representative proportion of the highly motile stages than the faster moving but smaller Gulf V sampler (Barkley, 1964).

The slopes of the catch curves shown in figure 6 appear to vary. For comparing these apparent variations in survival, we have calculated the gross survival between selected stages for each of the 10 stations. Distributions of gross survival values between first and third protozoaeae, third protozoaeae and third mysids, and third mysids and two-spine postlarvae are plotted in figure 7a, b, and c. Choice of these stages for the calculations was dictated by the anomalies that appeared

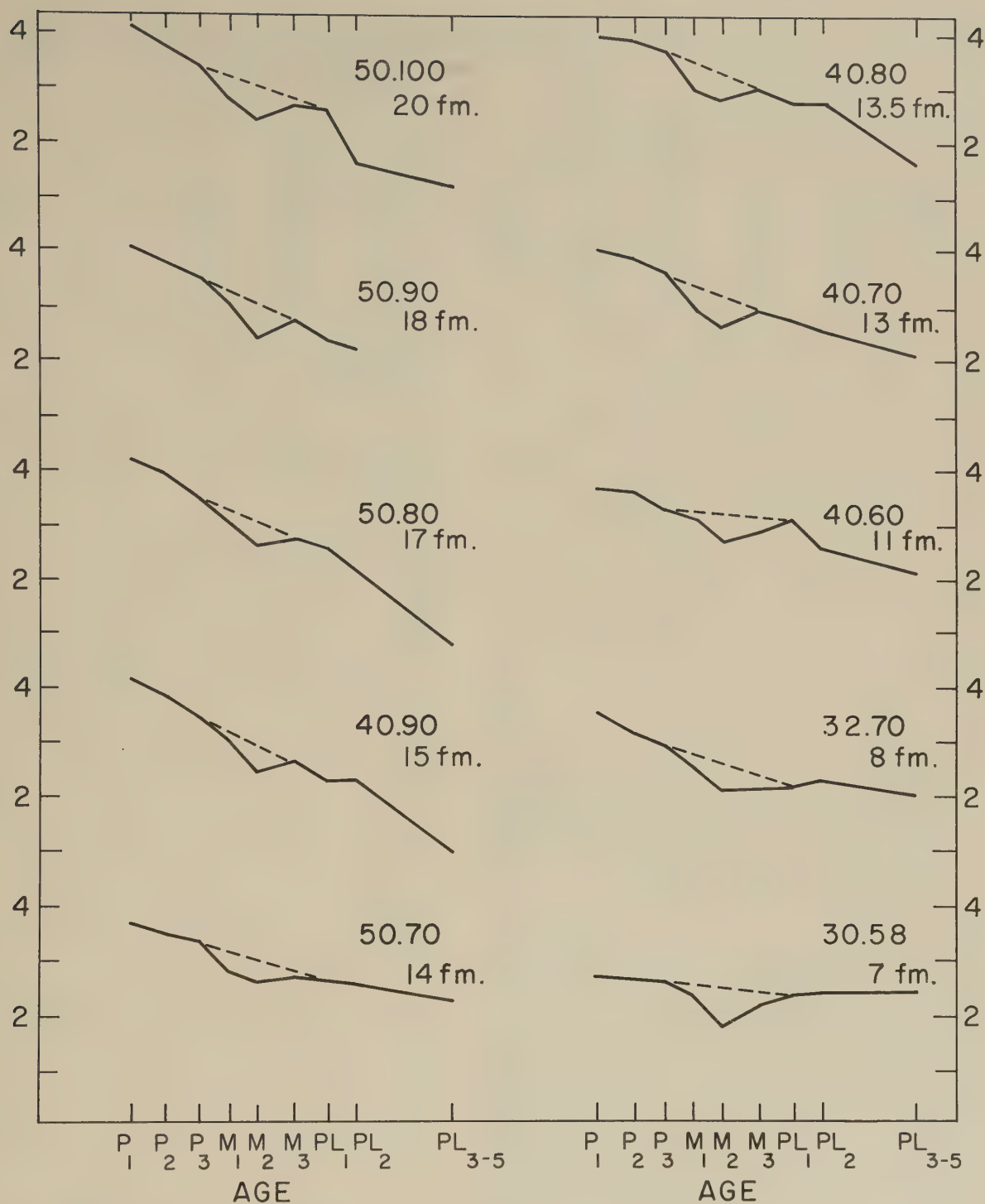


FIGURE 6.—Catch curves for larvae and postlarvae of *P. duorarum* based on the total catch at 10 stations on the Tortugas Shelf, August 1962 to October 1964. P₁, P₂, P₃=1st, 2d, and 3d protozoal stages; M₁, M₂, M₃=1st, 2d, and 3d mysis stages; P₁₁, P₁₂, P₁₃₊₅=1-, 2-, and 3- to 5-spine postlarval stages. Stages are distributed along abscissa relative to the mean age of each larval stage.

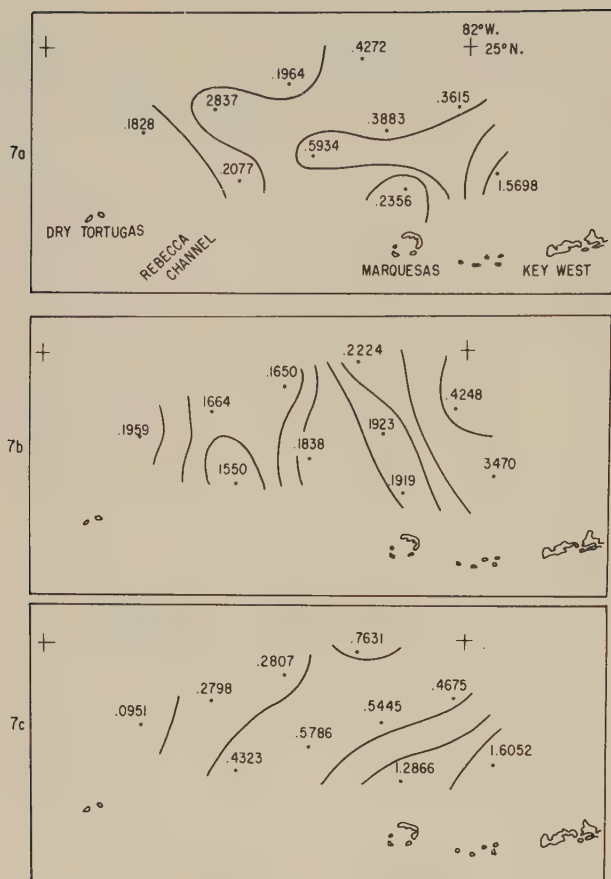


FIGURE 7a, b, and c.—Variations in apparent gross survival of larval and postlarval *P. duorarum* at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964: (a) 1st protozoal to 3d protozoal stage, (b) 3d protozoal to 3d mysis stage, and (c) 3d mysis to 2-spine postlarval stages.

in the catch curves and which have been discussed above. Lowest apparent survival was consistently in the deepwater stations in the northwestern sector of the sampling area, and greatest apparent survival (in some cases exceeding 100 percent) was in the southeastern sector. It appears highly unlikely that the calculated values are real values and that survival of larvae is greater in the southeastern sector. These consistent differences are probably a result of the migration of larvae away from the center of spawning. Stations 40.90 and 50.80 are believed to represent the centers of spawning, and the larvae disperse from this center.

Calculated daily survival rates between successive larval stages at each of the 10 stations are given in table 8. Total survival between first

protozoal and one-spined postlarval stages also is given (right-hand column); the highest rate of survival between these stages is usually at the shallowest, more easterly stations (fig. 8).

Because the dispersal of larvae from the center of spawning appears to affect the survival estimates pertaining to specific stations, it is difficult to estimate the true survival rate. Calculations of survival rate based upon the total catch of successive stages in relation to the total catch of first protozoae will have validity, however, provided it can be assumed that the main route of dispersal is over the area covered by the sampling stations (table 9).

If estimates of survival rates between first protozoa and first and second mysis are discarded, all remaining estimates are nearly constant and range from 78.6 to 82.0 percent (mean, 80.4 percent) per day.

Postlarvae enter the Everglades nursery grounds in the six-spine stage (Tabb, Dubrow, and Jones, 1962). On the basis of age data provided by Ewald (1965), these larvae are about 35 days old. At a survival rate of 80.4 percent per day, the fraction of the original population which survives to enter the nursery grounds can be estimated at 0.804^{35} , or 0.05 percent. The fraction of the original population of first protozoae (average age 5 days)

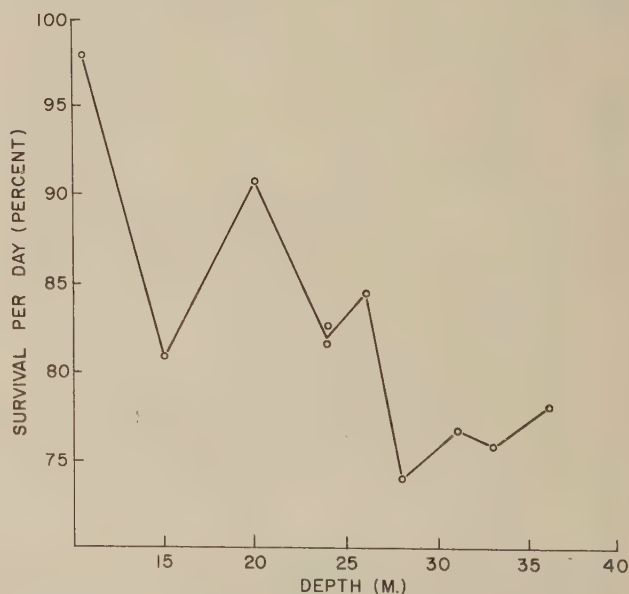


FIGURE 8.—The relation at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964, between depth and apparent survival rates of *P. duorarum* between 1st protozoal and 1-spine postlarval stages.

TABLE 8.—Calculated daily survival rates between successive larval and postlarval stages of *P. duorarum* at 10 sampling stations on the Tortugas Shelf

Station	Depth	Stages ¹								
		P ₁ -P ₂	P ₂ -P ₃	P ₃ -M ₁	M ₁ -M ₂	M ₂ -M ₃	M ₃ -P ₁	P ₁ -P ₂	P ₂ -P ₃₊₅	P ₁ -P ₁
	M.	Fractional survival per day								
50.100	36	.7311	.6898	.5228	.6585	1.2690	.9080	.3459	.8752	.7803
50.90	33	.7732	.7800	.5229	.5282	1.3090	.6858	.8468	-----	.7578
50.80	31	.7546	.6860	.5895	.6328	1.1160	.8582	.6409	.6354	.7678
40.90	28	.7496	.7081	.6166	.5330	1.2090	.6963	1.0350	.6884	.7396
50.70	26	.8098	.8849	.5508	.8513	1.0360	.9640	.9139	.9040	.8439
40.80	24	.9198	.8790	.5214	.7382	1.1800	.8067	.9965	.6814	.8269
40.70	24	.8708	.7796	.4977	.7008	1.2430	.8756	.8710	.8370	.8158
40.60	20	.9786	.6589	.8880	.6159	1.1790	1.2090	.5392	.8437	.9072
32.70	15	.7399	.7597	.6769	.6284	1.0650	1.0230	1.1000	.9137	.8098
30.58	11	1.2150	.9683	.7132	.5501	1.4230	1.1250	1.0950	.9979	.9786

¹ P₁, P₂, P₃=1st, 2d, and 3d protozoal stages; M₁, M₂, M₃=1st, 2d, and 3d mysis stages; and P₁, P₂, P₃₊₅=1-, 2-, 3- to 5-spine postlarval stages.

TABLE 9.—Estimated daily survival rates of larval *P. duorarum* over successively longer intervals on the Tortugas Shelf, August 1962 to October 1964

Stages ¹	Duration between stages	Calculated daily survival rate
	Days	Percent
P ₁ -P ₂ -----	2.70	0.8074
P ₁ -P ₃ -----	5.00	.7856
P ₁ -M ₁ -----	7.10	2.7247
P ₁ -M ₂ -----	9.25	2.7031
P ₁ -M ₃ -----	11.90	.7898
P ₁ -P ₁ -----	14.40	.8112
P ₁ -P ₂ -----	16.40	.8087
P ₁ -P ₃₊₅ -----	23.40	.8202

¹ P₁, P₂, P₃=1st, 2d, and 3d protozoal stages; M₁, M₂, and M₃=1st, 2d, and 3d mysis stages; and P₁, P₂, P₃₊₅=1-, 2-, and 3- to 5-spine postlarval stages.

² Estimates affected by sampling error.

would be 0.804³⁰, or 0.14 percent. In 1963, about 60,500×10⁸ first protozoae were produced within the sampling area; at the postulated rate of survival, about 85×10⁸ six-spine postlarvae would enter the nursery grounds. The total commercial catch of *P. duorarum* adults in the Tortugas area during 1963 was about 500 million individuals (U.S. Fish and Wildlife Service, 1964), implying that about 6 percent of the postlarvae may survive to be captured when they move to the trawling grounds as juveniles and adults.

Owing to the lunar periodicity of spawning, the proportions of larval stages in the catch change constantly, and we cannot estimate the survival rate operating at a given time nor obtain any information on the effect of temperature on survival.

DIRECTION OF MIGRATION

The data on survival rate shown in figures 7 and 9 indicate that the migration pattern of the larvae radiates away from the centers of spawning and that the apparent drift is mainly in an easterly direction. Jones et al. (footnote 6) showed that

few larvae are present north and west of our area of study. Koczy, Rinkel, and Niskin (1960) investigated the current system of the region and concluded that, although the water masses are subjected to a tidal movement of 9 to 11 km. per day, the resultant movement over a full tidal cycle is slight. Also, the small resultant drift is in a westerly direction and not in the required easterly direction. Additional evidence regarding the current system has been obtained recently through the release and recovery of seabed drifters. A vector analysis of the seabed drifter returns has indicated the presence of a slow southwest drift over the shrimp grounds. The detailed results have been reported by Rehrer, Jones, and Roessler (1967). The conclusions drawn from these results are that direct dispersal to the east seems improbable and that postlarvae reaching the nursery grounds of the Everglades are carried there by currents via some indirect route.

The most likely alternative means of larval transportation is by the Gulf Stream, passing through the Florida Straits. Biologists on cruises to the Tortugas region have on many occasions reported a strong southerly current flowing through Rebecca Channel and entering the Florida Straits. Current speed was measured on one occasion at 2.6 km. per hour (1.4 knots). Because Rebecca Channel is directly southwest of the centers of spawning (stations 40.90 and 50.80), considerable numbers of larvae must be swept through the channel and into the Florida Straits.

A survey cruise in October 1964 covered an area of some 10,789 km.² between Cape Sable on the Florida mainland and the Tortugas shrimp fishing grounds (fig. 10). Additional stations were in the Florida Straits south of the Florida Keys.

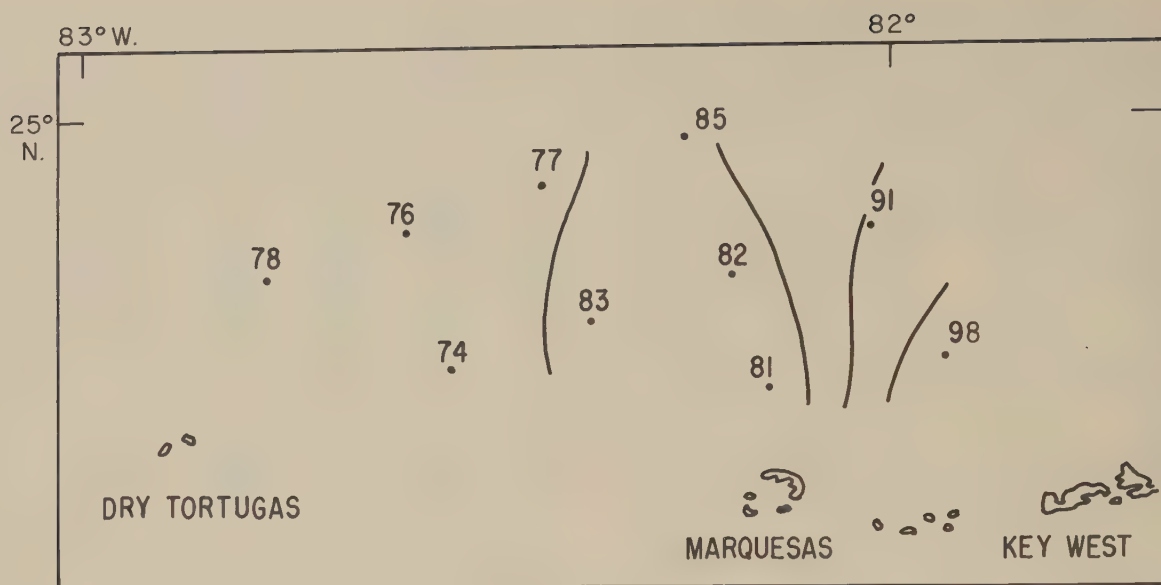


FIGURE 9.—Variations in the apparent daily survival rate between 1st protozoal and 1-spine postlarval stages of *P. duorarum* on the Tortugas Shelf, August 1962 to October 1964.

The most striking feature of figure 10 was the capture of large numbers of *P. duorarum* larvae, mainly protozoae, in the Florida Straits. These larvae were taken in the surface and midwaters of the Straits in water between 50 and 180 m. (28 and 98 fathoms) deep and at all the stations occupied. In contrast, few larvae or postlarvae were taken north of the Florida Keys.

We can, therefore, postulate that larvae are dispersed by transport out of Rebecca Channel and into the Florida Straits. The larvae would be carried eastward by the Florida Current and eddied back into the Florida Bay region by tidal currents moving through the inlets between the Florida Keys. If this transport does occur, the larvae would arrive at a point only about 37 to 56 km. from the Everglades nursery grounds, about 6 days after their exit from Rebecca Channel (calculated according to the velocity of the margins of the Florida Current given by Sverdrup, Johnson, and Fleming, 1942). The main part of the journey from the spawning grounds to the Everglades might take only a short time, leaving the bulk of the larval and postlarval life for the journey across Florida Bay, a distance of 37 to 56 km.

We have learned that postlarvae appear to react to tidal currents and ascend into the moving tide mainly during the nighttime flood tide. If this is so, movement across Florida Bay, where the

tides flow roughly north and south, might be accomplished within a week. If this migration takes place, the estimates of survival given in the preceding section must be reconsidered. We have shown that the apparent survival rate increases steadily toward the eastern sector of the sampling grounds (fig. 9). If larvae are removed from Tortugas grounds via Rebecca Channel, then their greatest loss through the channel would occur at stations nearest to the channel (viz, the western stations), and the apparently low rates of survival in this area are caused by loss of older larvae and not by movement of larvae in an easterly direction. This loss might explain the anomalous catches at station 32.70 (directly north of the Marquesas) which yield estimates of survival that are not of the same order as those calculated for station 30.58 (fig. 7a), although the stations are only 18.5 km. apart and of similar depths (14.5 and 11 m. or 8 and 6.1 fathoms, respectively). If larvae have traveled from the spawning grounds via the Florida Current, and then have been eddied back into the vicinity of station 30.58 via tidal currents in the Northwest Channel, the high proportion of older larvae and postlarvae at this station could be explained. The position of station 32.70, directly north of the Marquesas and away from any tidal channels, would preclude it from receiving older larvae.

5. Intramonthly variations in abundance of larvae are related to moon phase. Most spawning occurred during the waning moon (15-29 days after new moon).

6. Survival rates are nearly constant throughout the postnaupliar larval life, averaging about 80.4 percent per day. Differences in the apparent rate of survival at different sampling stations are caused by immigration and emigration of larvae between stations, by losses of larvae from stations in the path of currents which move into the Florida Straits, or by a combination of both.

7. Recoveries of seabed drifters confirm previous observations that currents in the sampling area are small (probably less than 1.8 km. per day), and that the movement of water is primarily toward the south and west. It is unlikely that larvae disperse directly toward the Everglades in the east. Available evidence indicates that dispersal may be effected primarily by the current which leaves the Tortugas area through Rebecca Channel, and enters the Florida Current in the Florida Straits. Entry into the Florida Current would result in rapid transport to the area adjacent to Florida Bay. If this migration route is the main method of dispersal and transport of larvae, then the average apparent rate of survival of 80.4 percent per day may be an underestimate, and the true rate of survival may be as high as 83 percent per day.

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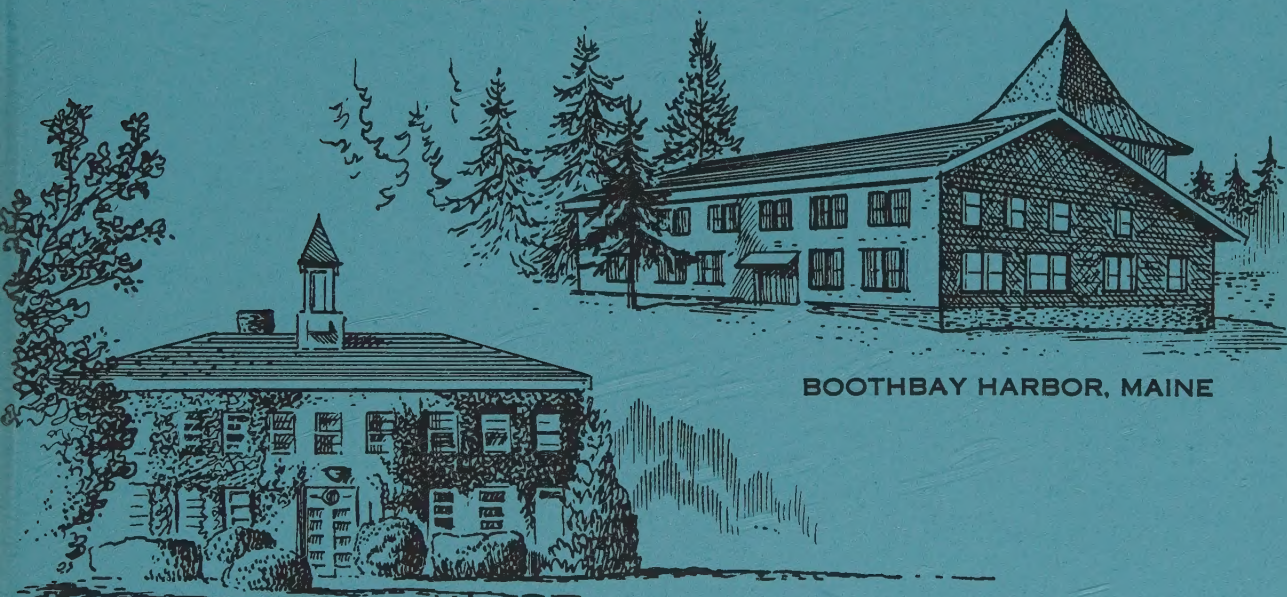
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